THE

PHYSIOLOGICAL ANATOMY AND PHYSIOLOGY OF MAN.

J. Stearns Jr.

THE

PHYSIOLOGICAL ANATOMY AND PHYSIOLOGY OF MAN.

BY

ROBERT BENTLEY TODD, M.D., F.R.S.

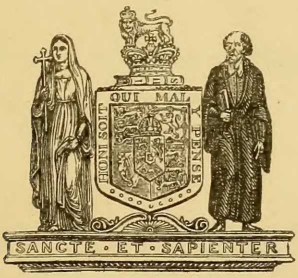
FELLOW OF THE COLLEGE OF PHYSICIANS, AND PHYSICIAN TO KING'S COLLEGE HOSPITAL;

AND

WILLIAM BOWMAN, F.R.S.

FELLOW OF THE COLLEGE OF SURGEONS, SURGEON TO KING'S COLLEGE HOSPITAL AND THE ROYAL LONDON OPHTHALMIC HOSPITAL,

LATE PROFESSORS OF PHYSIOLOGY AND GENERAL AND MORBID ANATOMY IN KING'S COLLEGE, LONDON.



IN TWO VOLUMES.

VOL. II.

LONDON:

JOHN W. PARKER AND SON, WEST STRAND.

1856.

LONDON:
PRINTED BY J. WERTHEIMER AND CO.,
CIRCUS PLACE, FINSBURY CIRCUS.

TO

SIR BENJAMIN COLLINS BRODIE, BART.,

D.C.L., F.R.S., ETC., ETC.,

CORRESPONDING MEMBER OF THE INSTITUTE OF FRANCE,
SERJEANT SURGEON TO THE QUEEN,

WHOSE MIND,

EARLY TRAINED IN PHYSIOLOGICAL RESEARCHES,

HAS BEEN DEVOTED

THROUGH A LONG LIFE OF EMINENT USEFULNESS

TO THE PRACTICE AND IMPROVEMENT

OF THE HEALING ART,

THIS WORK IS DEDICATED

BY

THE AUTHORS.

PREFACE.

The work, which is now brought to a conclusion, was commenced in the year 1843, having been designed as a text-book for the lectures on General Anatomy and Physiology, given in King's College, London.

In its title, we adopted the term *Physiological* Anatomy, in preference to the older one of *General*, or the later one of *Histological*, as being more comprehensive than either, and as denoting precisely that kind of anatomy, a knowledge of which is especially required for the investigation of those subjects which ought to come under consideration in a Physiological course.

We proposed to ourselves to give such a view of the main facts and doctrines of Anatomy and Physiology, particularly of those bearing on practical Medicine and Surgery, as might suffice for the wants of the student and

practitioner. Following that great master, Haller, we were desirous of giving to Anatomy a greater degree of prominence than had been usual in Physiological works, under the conviction that a thorough training in its several branches, descriptive, physiological, and comparative, is necessary to the formation of those habits of mind, which best fit their possessor for the successful investigation and the correct appreciation of physiological science. And we aimed at resting our anatomical descriptions, at least as regards the more important points, upon our own investigations, and at repeating former experiments, or devising new ones, whenever questions of sufficient interest presented themselves.

While we must humbly confess how small have been the advances attributable to our own labours, the immense extension given to the sciences of Anatomy and Physiology during the last fifteen years, may be admitted as some explanation of the delay that has occurred in the publication of our work, a delay that has been a constant source of regret to us, since we began to discover how impossible it would be for us to complete it within the term originally contemplated. That, in spite of repeated procrastination, it should have been so favourably received, both at home and abroad, has been the greatest encouragement to us, and demands our most thankful acknowledgments. If, indeed, our pursuits had tended to no other end than the cultivation of science, this book might have been finished

long ago; but the increasing interruptions incident to a professional life, and the large demand made on us by studies of a practical kind, began at an early period to impede our progress. These hindrances did not diminish as time wore on, nor were they lessened by the fact of the authorship being in the hands of two persons, however cordially united by common views and the ties of friendship, or by the necessity for frequent and prolonged conferences which that double authorship entailed.

Such is the apology we have to offer for the tardy completion of our work. It will, we doubt not, be fully appreciated by candid men who know by experience how multifarious are the calls made upon those who not only are candidates for professional employment in London, but hold also the responsible position of public teachers in a large School and Hospital.

Were it not indeed for the kind and valuable co-operation of Dr. Beale, who is now the sole occupant of the physiological chair in King's College, we should not even yet have been released from our difficulties. Dr. Beale, knowing all our views, and having worked with us on many points, has given us very important assistance in drawing up the concluding chapters of the work. Our warmest thanks are due to our friend and colleague for the patient industry and admirable judgment, with which, stepping out of his proper path of independent investigation, he has carried out our intentions, and enabled us,

although at the eleventh hour, to fulfil our engagement to our pupils and to the public.

To our friend Dr. H. Hyde Salter we are indebted for several excellent drawings, as well as for other valuable assistance.

We desire also to express our thanks to Mr. Vasey for the skill and ability with which he has executed his portion of the task, that of engraving the drawings on wood.

W. B. —— R. B. T.

London,
December 1*st*, 1856.

CONTENTS OF THE SECOND VOLUME.

CHAPTER XVI.

INNERVATION, CONTINUED.

CHAPTER XVII.

INNERVATION, CONTINUED.

CHAPTER XVIII.

INNERVATION, CONTINUED.

CHAPTER XIX.

INNERVATION, CONTINUED.

CHAPTER XX.

INNERVATION, CONTINUED.

CHAPTER XXI.

INNERVATION, CONTINUED.

CHAPTER XXII.

DIGESTION.

CHAPTER XXIII.

DIGESTION, CONTINUED.

CHAPTER XXIV.

DIGESTION, CONTINUED.

CHAPTER XXV.

DIGESTION, CONTINUED.

CHAPTER XXVI.

ABSORPTION.

CHAPTER XXVII.

THE BLOOD.

CHAPTER XXVIII.

THE CIRCULATION OF THE BLOOD.

CHAPTER XXIX.

RESPIRATION.

CHAPTER XXX.

ANIMAL HEAT.

CHAPTER XXXI.

VOICE.

CHAPTER XXXII.

SECRETION.

CHAPTER XXXIII.

SECRETING GLANDS.

CHAPTER XXXIV.

SECRETING GLANDS, CONTINUED.

CHAPTER XXXV.

DUCTLESS GLANDS.

CHAPTER XXXVI.

GENERATION.

CHAPTER XXXVII.

GENERATION, CONTINUED.

CHAPTER XXXVIII.

GENERATION, CONTINUED.

CHAPTER XXXIX.

GENERATION, CONTINUED.

CHAPTER XL.

GENERATION, CONTINUED.

CHAPTER XLI.

DEVELOPMENT.

CHAPTER XLII.

DEVELOPMENT, CONTINUED.

CHAPTER XLIII.

DEVELOPMENT, CONTINUED.

CHAPTER XLIV.

LACTATION.

ILLUSTRATIONS TO THE SECOND VOLUME.

THE

PHYSIOLOGICAL ANATOMY

AND

PHYSIOLOGY OF MAN.

CHAPTER XVI.

OF SMELL.—CAVITIES OF THE NOSE.—STRUCTURE OF THE NASAL MUCOUS MEMBRANE.—OLFACTORY REGION.—NERVES OF THE NOSE.—CONDITIONS OF SMELL.

This sense, designed to acquaint us with the odorous qualities of particles suspended or dissolved in the atmosphere, is seated in a portion of the nasal mucous membrane to which the air has access during ordinary breathing, and it may fairly be regarded as appended to the respiratory organ, much as the sense of taste has been seen to pertain to the digestive apparatus. But though it may serve to protect the lungs from the inhalation of deleterious gases, its principal use appears to be that of seconding the impressions of taste in conveying intelligence of the properties of food; for it almost invariably happens, that food possessing a decided flavour has likewise a not less characteristic smell.

Unlike the organs of touch and taste, that in which smell resides has no capacity of movement in relation to its ordinary stimuli; a deficiency quite supplied by the expansion of the chest in breathing, which carries the stream of odorous particles over the sentient surface.

The nose consists, 1, of two chief cavities or *nasal fossæ*, separated from one another by a vertical, bony, and cartilaginous septum, and each partially subdivided, by the spongy or turbinated bones, projecting from the outer wall, into three passages or *meatuses:* and, 2, of subordinate chambers, cells, or *sinuses*, of irregular size, hollowed principally in the ethmoid, sphenoid, frontal, and su-

perior maxillary bones, and communicating by narrow apertures with one or other meatus.

The *nasal fossæ* are lofty and of considerable depth, but much narrowed in lateral extent by the projection of the spongy bones towards the septum, which they almost touch. They open in front by the *nostrils*, which, by their horizontal position, direct the air, as it enters, towards the upper region, where the sense of smell is developed: behind, they lead, through a vertical slit on each side, the *posterior nares* or nostrils, into the upper compartment of the pharynx, above the soft palate, into which the food never penetrates, which is strictly a part of the respiratory tract, and which communicates through the Eustachian tubes with the middle ear. The nostrils, as parts of the countenance, and placed as safeguards at the commencement of the air-passages, are more elaborately organized than the posterior nares, which indeed are simple communications, without anything remarkable in their construction, except the shelving of the floor of the nose into the upper surface of the soft palate, favouring the gravitation of mucus from the nose into the pharynx. The nostrils have a cartilaginous framework, which keeps them open, unless forcibly compressed. This framework consists of five principal pieces: one in the middle, the *septal* cartilage, *a*, completing the septum in front; and two on each side, the *lateral* and *alar* cartilages, *b*, *c*, forming respectively the side of the nose below the nasal bones, and the wing of the nose. The former of these is triangular, and rests against the front edge of the septal cartilage; the latter is thinner and more flexible, and curved upon itself to form the dilatable chamber just within the nostril. Several loose nodules or flakes of cartilage frequently exist in connexion with the alar cartilages. The nostrils are further supplied with three pairs of muscles; viz. that called by Albinus *compressor naris*, but which is rather a lateral dilator, the *levator* and *depressor alæ nasi*. By these the orifices are dilated when we sniff the air in smelling, as well as under the influence of certain passions. The integuments of the nose are studded with the orifices of sebaceous follicles, which are among the largest in the body, and so numerous as to form a thick continuous layer under the cutis; and immedi-

Fig. 102.

Front view of the cartilages of the nose. Above is seen the outline of the nasal bones.—*a*. Front edge of the septal cartilage. *b*, *b*. Lateral cartilages. *c*, *c*. Alar cartilages, with their appendages.—After Sœmmerring.

ately within the nostrils is a growth of strong hairs, or *vibrissæ*, designed to obstruct the entrance of injurious substances.

With regard to the interior of the nose, its cavities are formed of bone, generally thin, compact, and laminated, everywhere invested with periosteum. This latter is lined with mucous membrane, the *Schneiderian* or *pituitary membrane*, continuous with the skin of the face at the nostrils, with the mucous covering of the eye through the lachrymal passages, and with that of the pharynx and middle ear through the posterior nares.

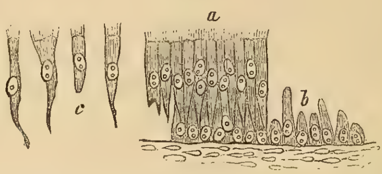
The mucous membrane of the nose varies in its structure in different regions. In many situations, especially in the sinuses, it is so intimately connected with the periosteum that that fibrous membrane is in fact a submucous areolar tissue; and the entire lining of the bone has been sometimes called a fibro-mucous membrane, which as a whole, is delicate in the extreme. On the septum and spongy bones, bounding the direct passage from the nostrils to the throat, the lining membrane is much more thick, partly in consequence of a multitude of glands being disseminated beneath it, and opening upon it, but chiefly perhaps from the presence of ample and capacious submucous plexuses of both arteries and veins, of which the latter are by far the more large and tortuous. These plexuses, lying, as they do, in a region exposed more than any other to external cooling influences, appear to be designed to promote the warmth of the part, and to elevate the temperature of the air on its passage to the lungs. They also serve to explain the tendency to hemorrhage from the nose in cases of general or local plethora.

In the vicinity of the nostrils the mucous membrane exhibits papillæ, and a scaly epithelium, like the corresponding parts of the skin. In the sinuses and in all the lower region of the nose, the epithelium is of extreme delicacy, being of the columnar variety, and clothed with cilia. This being the first occasion on which we have had to speak of this kind of epithelium, we shall briefly describe its structure and mode of growth.

The nucleated particles of which it consists are found in a double series: of which the first, resting on a subjacent basement tissue, is as yet imperfect; and the second, rising to and forming the free external surface of the membrane, is completely developed, and furnished with cilia. The deeper series is the more adherent, and if recent will be found to remain more or less attached, when the superficial and perfect layer has been removed by a gentle stream of water. It will then have the appearance represented at *b*, fig. 103. The nuclei which are arranged nearly on the same level, are ovoid,

and contain usually two nucleoli, even more pellucid than themselves. The surrounding substance is in relatively small quantity, and is seen either as a mere film around the nucleus, or vertically elongated in various degrees. In the superficial series, *a*, the nuclei, though lying on the same general level, are placed some higher and some lower, as if for convenience of package, since the particles bulge where the nuclei are situated. The nuclei are scarcely

Fig. 103.



View of the ciliated epithelium of the nose, seen in section: *a*. Superficial series, clothed with cilia. *b*. Deeper series, becoming elongated vertically. *c*. Various shapes of the perfect ciliated particles.—Magnified 180 diameters.

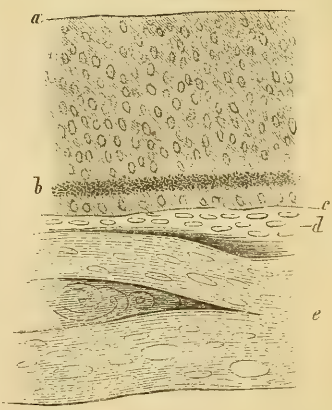
different in size or shape from those below. The surrounding granular substance of the particle is, however, much longer than before; below, where it is implanted between the particles of the deep series, it is pointed, though sometimes blunt, and often club-shaped, while the upper end enlarges, and terminates by a flat surface, from which the cilia project, *c*. It must be observed, that the cell-membrane, so apparent in the scaly epithelium heretofore described, is not to be found in this variety. It is either early absorbed, or else so delicate and so united to the contained substance as not to be distinguishable as a separate object.

It appears clear that this double series of particles constitutes two stages of growth of the same structure. Instances are not wanting of particles intermediate between the two, in which the future surface of the membrane is marked by a horizontal line, above which the granular substance exhibits a vertically fibrous structure, indicative of the coming cilia. Moreover, we have met with examples in which a surface perfectly ciliated was still covered with a layer of other ciliated particles, that, from their half-dissolved appearance, had evidently passed their prime, and were in process of decay. This progressive developement of the particles as they recede from the vascular source of their nutriment, and especially the evolution at last of those delicate evidences of life, the ciliary appendages, is a glaring example of the essential independence of the vitality of the tissues on the blood-vessels, and makes it more easy to conceive the really subordinate or ministerial office of those channels.

We now come to the proper seat of the sense of smell, a comparatively limited district of the nasal organ, to which we shall apply the term, *olfactory region*. As this olfactory region has not hitherto been distinguished, nor its character understood, we shall describe it somewhat minutely. This, as well as other parts, can be best examined in animals, because they can be procured fresh and in a state of health. The mucous membrane so soon loses many of its most interesting features, especially where death has followed on chronic disease, that the human subject is not the most favourable for the investigation of its physiological anatomy, and can only be advantageously inspected after the lower animals have furnished the general clue. This remark is well illustrated by the present instance.

The olfactory region is situated at the top of the nose, immediately below the cribriform plate of the ethmoid bone, through which the olfactory nerves reach the membrane; and it extends about one third, or one fourth, downwards on the septum, and over the superior and part of the middle spongy bones of the ethmoid. Its limits are distinctly marked by a more or less rich sienna-brown tint of the epithelium, and by a remarkable increase in the thickness of this structure, compared with the ciliated region below; so much so, that it forms an opaque soft pulp upon the surface of the membrane, very different from the delicate, very transparent film of the sinuses and lower spongy bones. The epithelium indeed here quite alters its character, being no longer ciliated, but composed of an aggregation of superposed nucleated particles, of pretty uniform appearance throughout; except that, in many instances, a layer of those lying deepest, or almost deepest, is of a darker colour than the rest, from the brown pigment contained in the cells (fig. 104, *b*). These epithelial particles, then, are not ciliated; and they form a thick, soft, and pulpy stratum, resting on the basement membrane. The deepest layer often adheres after the others are washed away. On looking on the under surface of this epithelium, when it has been

Fig. 104.



Vertical section of the olfactory region of the nose of the Rabbit:—*a*. Surface of the epithelium. *b*. Layer coloured by pigment. *c*. Line of basement membrane. *d*. Nucleated tissue seen below. *e*. Olfactory nervous filament branching.—Magn. 250 diam.

detached, we observe projecting tubular fragments, similar to the cuticular lining drawn out of the sweat-ducts of the skin, when the cuticle is removed after maceration (figs. 79 and 80). In fact, glands apparently identical with the sweat-glands exist in this region in great numbers. They dip down in the recesses of the submucous tissue, among the ramifications of the olfactory nerves; and their orifices are very easily seen, after the general brown coat of epithelium has been detached, lying more or less in vertical rows, the arrangement of which is probably determined by the course of those nerves beneath. They become more and more sparing towards the limits of the olfactory region. The epithelium of these glands is bulky, and like that of the sweat-glands, contains some pigment. As the duct approaches the epithelium of the general surface, its wall becomes thinner and more transparent; and, in its subsequent course upwards, it is difficult to be traced, for it does not appear to be spiral, or its particles to differ from those which they traverse. We have sometimes seen rods of epithelium, apparently hollow, left projecting from the basement membrane, after the brown epithelium has been washed away; and these are perhaps portions of the excretory ducts of these glands.

A good injection of the nasal organ in the fœtus, both of man and animals, will display a multitude of minute capillary loops upon the surface of the olfactory region, bearing a close resemblance to those of rudimentary papillæ. These loops were first pointed out to us two years ago by Mr. Quekett in the fœtal pig, and also in the human fœtus at its full term; and so clearly did they seem to indicate the presence of true papillæ in this region, that we made repeated and close examinations of the recent organ, in order to expose their structure, supposing them to be concerned in the sense of smell. These researches, pursued on adult specimens, have been hitherto fruitless; at least, we have found no other evidence of papillæ than delicate hollow epithelial processes remaining, after a gentle current of water had washed away the principal portion of the brown epithelial investment— an appearance too ambiguous to be spoken of with confidence. In the human fœtuses we have injected, the loops are such as are represented above (fig. 105). The convexity of the loops presents a decided dilatation, being from $\frac{1}{2000}$ to $\frac{1}{1500}$ of an inch wide, while the diameter of the capillary on either side is only

Fig. 105.

Dilated loopings of the capillaries of the olfactory region of the Human Fœtus, injected and magnified.

about $\frac{1}{3000}$ inch. We have hitherto failed in seeing any loop-like or projecting capillaries in injections of adult specimens. Care must be taken not to confound these loops in the olfactory region of the fœtus with the loops of the undoubted true papillæ, situated just within the nostrils, and which belong to touch.

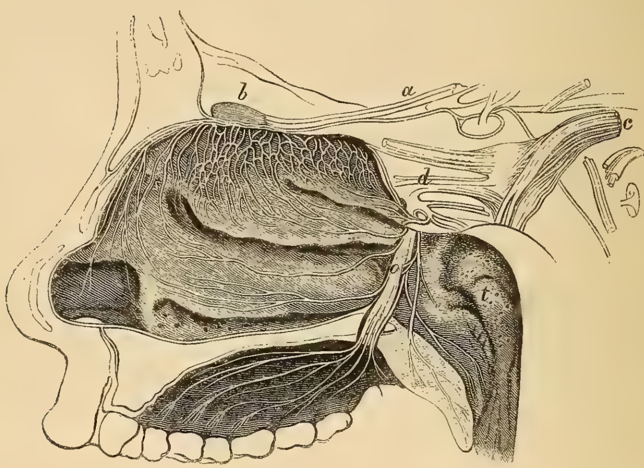
Of the Nerves of the Nose.—These are the first pair, and branches of the fifth pair, besides motor filaments from the facial nerve to the external muscles. The first pair has long been considered as the proper nerve of smell, though not without dispute. That it has been rightly so regarded, however, is evident for many reasons. Its limitation to the upper and middle spongy bones, to the roof of the nasal fossæ, and to the upper half of the septum, where the mucous membrane exhibits peculiar characters, and smell is principally, if not exclusively, exercised ; its development in the vertebrate class, proportionate, *cæteris paribus*, to the acuteness of smell, being largest in animals of keenest scent ; the loss of smell, without other effect, consequent on its division ; together with the perversion or loss of smell found in many authentic cases in connexion with disease of these nerves or their associated cerebral region : all these facts point irresistibly to this conclusion.

Of the First Pair.—Under this head are to be described the olfactory process or lobe, and the olfactory filaments distributed to the nose.

The *olfactory process*, or *lobe*, (*a*, *b*, fig. 106) is a slender prism of fibrous and vesicular nervous matter, terminating in front in a bulb ; and it is sunk in the fissure which bounds the supra-orbitar convolution on the under surface of the anterior lobe of the cerebrum (vol. i. p. 282). It is connected with the inferior surface of the brain by an external and internal root. The former is the longer, and may be traced in the nervous matter forming the floor of the fissure of Sylvius, and among the arteries of the locus perforatus, towards the lower and outer part of the corpus striatum, near the anterior commissure of the cerebrum. In the dog and cat, where this process is much larger, the anterior commissure seems to have a more intimate relation to the olfactory processes. In the same animals the white matter of the process is continuous also with that of the largely developed hippocampus major. The internal root winds inwards, and is lost in the gray matter in front of the optic commissure, near the anterior extremity of the corpus callosum. In front of the point where the roots join, there is a process of gray matter constituting a third or gray root, and which is continued forwards as a portion of the olfactory process, as far as the bulb where it expands.

The *bulb* of the olfactory process (fig. 106, *b*) is an elongated oval mass of nervous matter, which lies upon the cribriform plate. The white portions of the olfactory process terminate in its posterior extremity. It contains a small ventricle, which, in some of the lower

Fig. 106.



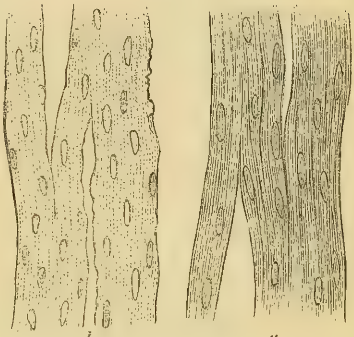
Outer wall of the nasal fossa, with the three spongy bones and meatus: the nerves being shown as they would appear through the membrane if it were transparent.—*a.* Olfactory process. *b.* Olfactory bulb (represented rather too short) resting on the cribriform plate. Below is seen the plexiform arrangement of the olfactory filaments on the upper and middle spongy bones. *c.* Fifth nerve within the cranium with its Gasserian ganglion. *d.* Its superior maxillary division, sending branches to Meckel's ganglion, and through that to the three spongy bones, where they anastomose with the olfactory filaments, and with *s*, branches of the nasal division of the ophthalmic nerve. *o.* Posterior palatine twigs from Meckel's ganglion, supplying the soft and hard palate. *t.* Orifice of the Eustachian tube on the side of the pharynx, behind the lower spongy bone.—From Sœmmerring, two-thirds diameter.

animals, is prolonged backwards as far as the cerebral ventricles. This ventricle is lined with a delicate white layer, but with this exception, the whole olfactory lobe consists of gray matter. In particular it is to be observed, that the under portion, which reposes on the cribriform plate, and sends down the olfactory filaments, contains no tubular fibres.

The *olfactory filaments* (figs. 106, 7, 8) are from fifteen to twenty-five in number, and, passing through the apertures of the cribriform plate, may be seen, invested with fibrous sheaths derived from the dura mater, upon the deep or attached surface of the mucous membrane of the olfactory region. They here branch and sparingly reunite in a plexiform manner, as they descend. They form a considerable part of the entire thickness of the membrane, and differ widely from the ordinary cerebral nerves in structure. They contain no white substance of Schwann, are not divisible into

elementary fibrillæ, are nucleated, and finely granular in texture, and are invested with a sheath of homogeneous membrane, much resembling the sarcolemma, or, more strictly, that neurilemma which we figured from the nerves of insects in the former volume, p. 226. These facts we have repeatedly ascertained, and they appear to be of great importance to the general question of the function of the several ultimate elements of the nervous structure, especially when viewed in connexion with what will be said on the anatomy of the retina. We are aware that some anatomists deny the existence of the white substance of Schwann as a natural element of the nerve-fibre in any case, pretending that it is formed by artificial modes of preparation; we hold it to be a true structure; but, however that may be, these nerves never exhibit it, however prepared. They rather correspond with the gelatinous fibres. Now there is no kind of doubt that they are a direct continuation from the vesicular matter of the olfactory bulb. The arrangement of the capillaries in well-injected specimens is a convincing proof of this, as these vessels gradually become elongated on the nerve assuming a fibrous character as it quits the surface of the bulb; and further, no tubular fibres can ever be discovered in the pulp often left upon the orifices of the cribriform plate after detachment of the bulb. It must be remembered, that a few tubular fibres from the nasal nerve of the fifth here and there accompany the true olfactory filaments, but these only serve to make the difference more evident by contrast.

Fig. 107.



Olfactory filaments of the dog:—*a*. In water. *b*. In acetic acid.—Magnified 250 diameters.

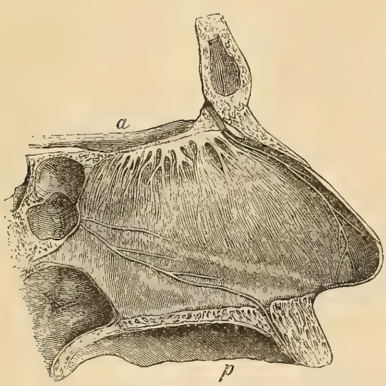
Although these nucleated olfactory filaments lie in great abundance under the mucous membrane of the olfactory region, we have been quite foiled in our attempts to trace their ultimate distribution in the membrane, and the difficulty is attributable to their want of the characteristic white substance. Their elongated nuclei render the larger branches unmistakeable; but if these become resolved at last into fibrous elements, the nuclei cease to be distinct from those of the numerous nucleated tissues which they traverse. In this respect they correspond, in all probability, with the nerves of some of the papillæ of the tongue (see vol. i. pp. 436-7); and, considering the similarity between the two senses, an argument may

be hence deduced for the limitation of the sense of taste to those elementary nerve-fibres going to the tongue which are without the white substance of Schwann. If this be so, the looped tubular fibres are confined to the impressions of touch in that organ.

We are averse from speculating prematurely on the meaning of anatomical facts, but as some hypothesis will intrude itself, we would venture to hint that this amalgamation of the elements of the peripheral part of the olfactory nervous apparatus in the larger branches, and probably in the most remote distribution, as well as the nucleated character indicative on an essential continuity of tissue with the vesicular matter of the lobe, are in accordance with the oneness of the sensation resulting from simultaneous impressions on different parts of this organ of sense, and seem to show that it would be most correct to speak of the first pair of nerves, as a portion of the nervous centre put forward beyond the cranium, in order that it may there receive, as at first hand, the impressions of which the mind is to become cognizant. No true tubular fibres belong to the olfactory nervous apparatus, except those commissural ones passing between the bulb and certain portions of the cerebrum.

The branches of the fifth pair given to the nose (figs. 106 and 108), are derived from its ophthalmic and superior maxillary divisions. The nasal twig of the former, crossing the orbit, passes over the cribriform plate of the ethmoid bone into the nose, in close contact with a portion of the olfactory nerve, and most probably forms some anastomosis with it. Its subsequent course is downwards, subdividing to supply the mucous membrane and skin in the neighbourhood of the anterior orifices. The pungent sensation preceding sneezing seems to be an affection of this twig, and the flow of tears that accompanies that act is accounted for by the common source of this and of the lachrymal nerve.

Fig. 108.



Nerves of the septum of the Nose:—*a*. Olfactory bulb resting on the cribriform plate, below which its branches may be traced on the septum about halfway down. Behind, the naso-palatine nerve from Meckel's ganglion is seen descending to the naso-palatine canal. In front, the nasal twig of the ophthalmic nerve descends towards the tip of the nose, dividing into two principal branches. *p*. Roof of the mouth. *e*. Orifice of the Eustachian tube.—From Arnold, one half diam.

The nasal branches of Meckel's ganglion enter the nose through the spheno-palatine foramen, or by pores between this and the pos-

terior palatine canal, and then spread over the three turbinated bones and the septum nasi, anastomosing at several points with the olfactory filaments, and with the nasal branch of the ophthalmic (figs. 106 and 108). When the fifth nerve is diseased, so that sensation is lost generally in the parts supplied by it, a brush may be introduced into the nostril, and rubbed over the surfaces usually so extremely sensitive, without the slightest discomfort to the patient. Similar effects follow division of the nerve. Hence it may be concluded that the fifth gives common sensibility to the nose, in common with most of the other parts which it supplies.

Conditions of smell.—In addition to the essential conditions of integrity of the nervous apparatus, and the presence of the requisite stimulus, a healthy condition of the epithelial investment of the papillæ seems necessary for perfect smell. If the mucous surface is dry, or if it is in the raw irritable state, attended with watery discharge, induced by cold, smell is impaired or lost. This is explained by considering the manner in which the nerves are ordinarily brought under the influence of the stimulus. As in taste, a solution of the stimulus in the surface of the membrane is requisite in order that the odorous substance may actually reach the nerve. Insoluble substances cannot be smelt. Hence, whether the membrane be too dry, or an inordinate excretion of fluid be going on from its surface, the necessary penetration of the stimulus to the nerves is alike interfered with. In the latter case, the effect may partly depend also on a change produced by the inflammatory action, in the excitability of the nerves themselves.

Since odorous substances must undergo solution before they can affect the olfactory nerves, why, it may be asked, cannot such substances, if dissolved in water and injected into the nose, be recognized by their smell? In answer to this it may be stated, that there is no reason to deny the possibility of their being so recognized, as far as the excitability of the nerves is concerned. But the ciliated epithelium of the nose, and the nerves of common sensation supplying the lining membrane, instantly resent the contact of all other fluids than the film which moistens the surface, and which is naturally furnished by it in due proportion to the exigencies of the part; and when the membrane is thus irritated, and its texture altered by the water, it need not excite surprise that its special sensibility should be altered or disguised. The organ of smell in fishes resembles that of air-breathing animals in every essential point of structure, and differs mainly in the habitual contact of its sentient surface with the surrounding water. It may there-

fore be concluded, that sensations of smell are excited in it by substances brought to it through the water, corresponding in kind with those brought in the other case through the air, but eventually dissolved in the moisture of the membrane. The nature of the sensation will depend on the special sensibility of the nerve, which in both cases can be excited only by the stimulating substance in solution ; and whether air or water brings the stimulus to the surface of the membrane, is made important only by the special adaptation of that surface to the contact of one or the other medium.

We may here notice two important reasons for the situation of the organ of smell, so high up in the nose, in addition to the obvious one of the protection from mechanical injury thus afforded to so delicate a part. These are, that it is thereby screened from the contact of air either too *cold* or too *dry*. The interposition between the outer orifice and the organ of smell of projecting and folded membranes of active secreting powers, and containing large reservoirs of blood (in the plexuses already described), seems designed to answer both these purposes. These parts break the force of the current, warm it, and impart that degree of moisture which is best calculated to aid the solution of the odoriferous particles on the sentient surface to which they are afterwards applied. The remarkable complexity of the lower turbinated bones in animals with acute scent, without any ascertained distribution of the olfactory nerves upon them, has given countenance to the supposition that the fifth nerve may possess some olfactory endowment, and seems not to have been explained by those who rejected that idea. If considered as accessory to the perfection of the sense in the way above alluded to, this striking arrangement will be found consistent with the view which limits the power of smell to the first pair of nerves.

We have already remarked that the exercise of the sense of smell is not attended with more than a general idea of locality. The sensation is even more simple in this respect than that of taste. Unless the experiment be made, we know not that we are constantly exerting the sense on two sides, for the double sensation is perceived as a single one. Our observations on the anatomy of the olfactory nervous apparatus may assist in the explanation of this fact.

The sense of smell may be voluntarily heightened by short and quick inspirations, which drive the air smartly against the upper region of the nose, and thus lead to the more effectual detention of its odoriferous particles by the membrane, while the attention is given to its sensations. On the other hand, by closing the nostrils, and breathing through the mouth, all access to the organ of smell is

prevented, except that gradually effected by admixture through the pharynx and posterior nares. It is through this latter channel that the odorous particles of food, rising from the throat to the nose during expiration, blend the sensation of smell with that of taste so strongly and habitually, that it becomes difficult to discriminate between them.

Analogy would lead to the belief that the nervous apparatus of smell, if irritated by an internal cause, would be the seat of olfactory sensations. Such *subjective* phenomena have been known to exist in certain cases of disease, in which the nerve, or the anterior lobe of the brain, has been afterwards found disorganized. Occasionally, too, odours are perceived without the actual presence of the object usually giving rise to them. These also must be regarded as subjective.

The quality of the sense, also, seems to vary not a little in different persons; some being strongly affected, even to faintness, by a scent which is almost imperceptible to others. The odours of flowers, for example, are very variously appreciated, as every one must have more or less observed. There are corresponding idiosyncrasies in the other senses.

On the subjects of this chapter, in addition to the elementary works before quoted, the following may be consulted:—Schneiderius, de osse cribriformi et sensu ac organo odoratus; Scarpa, de organo olfactus; also, de auditu et olfactu: Sœmmerring, Icones organi humani olfactus, 1809: H. Cloquet, Osphrésiologie, ou traité des odeurs. Paris, 1821.

CHAPTER XVII.

OF VISION.—OF THE ANATOMY OF THE EYEBALL, OPTIC NERVES, AND APPENDAGES.—OF THE PHENOMENA OF VISION.

It would appear that an animal may be sensible to light without possessing an organ of vision. Thus, that beautiful little polyp, the *hydra*, shows a decided predilection for the light side of the vessel in which it is kept. Most animals, too, require the presence of light for the full performance of their functions; and this is not the case with animals alone, but with plants likewise; both, in the great majority of instances, pine away in the dark, or fail to arrive at complete development.

But the presence of an *organ of vision* implies something more than the mere power of distinguishing between light and darkness. It must enable the animal to discern something of the colour, or at least of the form, of surrounding objects; and this in a degree proportioned to the perfection and complexity of its organization.

The principle on which the organ is constructed seems to be in all cases the same, viz. that of the *camera obscura*—a dark chamber with a small aperture for the admission of light, a quantity of black matter for the absorption of superabundant rays, and a nervous expansion on that wall which receives the rays of light.

Among the lower invertebrata, the eyes, or *ocelli*, consist only of a nervous point, shielded with a minute quantity of colouring matter. The chief additions which increase the complexity of these organs in the higher animals consist of transparent media and lenses for the refraction of the light, and the production of a more precise image; of an apparatus for the regulation of the quantity of light admitted to the retina; and of other appendages for protection and movement.

The position of the human eye at the upper part of the face and directed forwards, while it gives to the countenance its most important element of beauty, adds greatly to the utility of the organ, by increasing the visual range. For protection in this exposed situation it is sunk deeply in a cushion of fat, within a bony cavity, the *orbit*, the prominent borders of which are well-adapted to receive

the force of blows directed towards that region. It is furnished with muscles capable of moving it towards any side, and of protruding or sinking it. It is likewise provided with moveable lids to guard its exposed surface from mechanical injury, and its nerve from the effects of excessive light; and with a lachrymal apparatus, by which the front of it is continually irrigated with a bland fluid.

In the globe of the eye itself we recognize, as the most essential constituents, the expansion of the optic nerve, called the *retina;* and, in front of this, the *transparent refracting media* which, as a whole, transmit the light so as to bring its rays to a focus upon the nervous sheet. The curved form of the retina, and the rounded figure of the eye thence derived, are perfectly adapted to the curvatures of the refracting media: so that, if the nervous lamina had assumed any other shape, it would have been more or less out of focus, and vision consequently have been indistinct.

To maintain the figure of the retina, and to protect a part of so much delicacy, in which the slightest change of form would be attended with injury to the function, the whole is encased in a dense tunic of great strength, termed the *sclerotica* (σκληρὸς, durus), which is opaque, except in front, where it is modified in structure becomes perfectly transparent to allow the light to enter, and is known as the *cornea.* Between the sclerotica and the retina is interposed a layer of dark pigment, contained in a delicate membrane termed the *choroid.* In front of the retina are the *transparent media.* One of these (the *vitreous body* or *humor*) is contained immediately within the cup which the retina forms, and appears specially constructed to give it that necessary support inside, which the sclerotica furnishes on the outside. The vitreous body occupies four-fifths of the whole globe. Imbedded in its anterior part is a double convex lens (the *crystalline lens* or *body*), which comes nearly up to the cornea; leaving, however, a small cavity containing a watery fluid, the *aqueous humor*, between itself and that transparent part of the external case. Across this cavity, and dividing it into an *anterior* and *posterior* chamber, hangs a vertical curtain-like process of the choroid, called the *iris*, perforated in the centre by an aperture, *the pupil*, for the admission of light to the interior, and contractile under the influence of light on the retina, in order that it may regulate the amount of light entering the organ. The perfect fluidity of the aqueous humor is a provision to allow of the expansion and contraction of the pupil, and of the movements of the lens itself towards or from the cornea.

The human eye would be nearly globular were it not that the

anterior portion, formed by the cornea, is a part of a smaller sphere than the rest, and is therefore slightly protuberant. Hence the antero-posterior axis of the eye is longer than the transverse, in the proportion of twenty to nineteen.

In terrestrial quadrupeds its shape is for the most part nearly similar. In animals that inhabit the water, as Cetacea and fishes, the eye is considerably flattened in front; so that, in some fishes, it is almost a half-sphere. In birds, on the contrary, especially those which fly high, the cornea is very prominent compared with the rest of the eye, which is of a more or less flattened form. These differences have an evident reference to the density or rareness of the medium through which the light passes to the organ.

A more detailed description of the several structures composing the ball of the eye will now be given, in which we shall follow the order most natural to a dissector, viz. that from without, inwards.

The *sclerotic* coat consists of white fibrous tissue, in which, however, the ultimate filaments are more distinct, and less wavy than in ordinary specimens. These form numerous layers, crossing one another chiefly at right angles, and thus constitute a membrane capable of resisting distension, and of retaining its figure under pressure. It has a white glistening aspect, especially in front, where it receives the insertion of the tendons of the four straight muscles, and, being visible, is familiarly known as the "white of the eye." The sclerotic is thickest behind, and becomes gradually thinner in front, till nearly in contact with the cornea, where it increases in strength a little.

In the animal series, the sclerotic becomes of greater relative thickness behind, in proportion to the flattening of the organ in front, and the pressure which it will have to sustain from the surrounding medium. In aquatic mammalia this is effected simply by an accumulation of the fibrous tissue in that situation, as in the whale, where it is often an inch in thickness, a wonderful provision against the enormous pressure to which that animal is exposed at great depths. In reptiles and fishes there is a thick cartilaginous lamina included in the fibrous tissue; and in some this cartilage ossifies, as in the sea-bream, mentioned by Dr. Jacob. In birds too, where the sclerotica is flattened from before backwards, a thin cartilaginous plate exists in it, which confers a peculiar elasticity and firmness, and is at the same time light and slender. Its anterior part is further fortified by fourteen or fifteen osseous plates, disposed in a regular series round the margin of the cornea. Similar plates occur in various reptiles, and are especially remarkable in those gigantic specimens of this class, the Ichthyosauri and Plesiosauri, which are only known to us by their fossil remains.

The optic nerve comes through the sclerotic behind, at a distance of about its own breadth, or nearly one eighth of an inch, on the inner side of the axis of the eye, by which is meant the axis of the

dioptric media. This nerve contains a considerable quantity of fibrous tissue separating and supporting its fasciculi, and as it traverses the sclerotic this tissue becomes continuous with the borders of the aperture, so that the aperture itself may be said to be cribriform; the nerve passing through a number of distinct canals of fibrous tissue, before it reaches the inner surface of the sclerotic. It is indifferent whether this cribriform tissue be called neurilemma or sclerotic. One thing, however, may be always observed. The nerve, as it pierces the sclerotic, contracts, and lies in a smaller compass, so that the entire aperture is somewhat funnel-shaped, and wider behind than in front; and, though the nerve is moveable on its entrance into the sclerotic aperture, it is always fixed firmly at the inner surface of that aperture, where the retina commences.

The aperture in the sclerotic in front, for the cornea, is circular, and usually about $\frac{7}{16}$ths of an inch in transverse diameter, and rather less vertically, though in some individuals altogether smaller. Between the point of entrance of the optic nerve, and the attachments of the recti muscles, there are several minute apertures for the transmission of vessels and nerves to the interior. The nutrition of this tunic itself is provided for by small vessels ramifying on its surface, and sparingly continued into its substance. Its own proper vascularity does not seem to be greater than that of other fibrous structures.

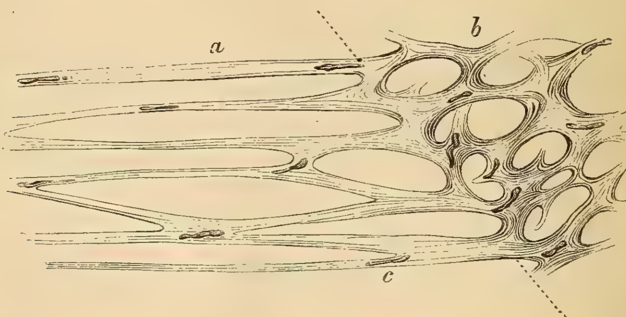
Of the Cornea.—The size and shape of this transparent part of the outer case of the eye have been already indicated. It is spherical rather than spheroidal, and its posterior surface is of parallel curvature with the anterior; so that it does not appear to be a meniscus lens, thicker in the middle, as some authors have described: this at least is the result of our careful examination. The cornea, when its concavity is filled up with the aqueous humor, is of course a powerful converger of the rays of light towards the iris, and through the pupil to the lens. Viewed from within, its circumference is exactly circular; but on the outside it generally appears wider transversely, from the sclerotic, which overlaps it on all sides, encroaching upon it rather more above and below. The cornea and sclerotic are firmly connected by continuity of texture, and cannot be disunited even by maceration. The cornea is possessed of great toughness, and will even resist a force capable of rupturing the sclerotic.

The cornea, though a beautifully transparent substance, and appearing at first sight as homogeneous as glass, is nevertheless full of

elaborate structure. It is in fact composed of five coats or layers, clearly distinguishable from one another. These are, from before backwards, the *conjunctival layer of epithelium*, the *anterior elastic lamina*, the *cornea proper*, the *posterior elastic lamina*, and the *epithelium of the aqueous humor*, or *posterior epithelium*. The cornea, when uninflamed, contains no blood-vessels; those of the surrounding parts running back in loops, as they arrive at its border.

On the *cornea proper*, or *lamellated cornea*, the thickness and strength of the cornea mainly depend. It is a peculiar modification of the white fibrous tissue, continuous with that of the sclerotic. At their line of junction (fig. 109), the fibres, which in the sclerotic

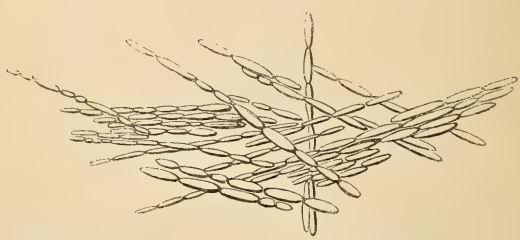
Fig. 109.



Vertical section of the Sclerotic and Cornea, showing the continuity of their tissue between the dotted lines:—*a*. Cornea. *b*. Sclerotic. In the cornea the tubular spaces are seen cut through, and in the sclerotic the irregular areolæ. Cell-nuclei, as at *c*, are seen scattered throughout, rendered more plain by acetic acid.—Magnified 320 diameters.

have been densely interlaced in various directions, and mingled with elastic fibrous tissue, flatten out into a membranous form, so as to follow in the main the curvatures of the surfaces of the cornea, and to constitute a series of more than sixty lamellæ, intimately united to one another by very numerous processes of similar struc-

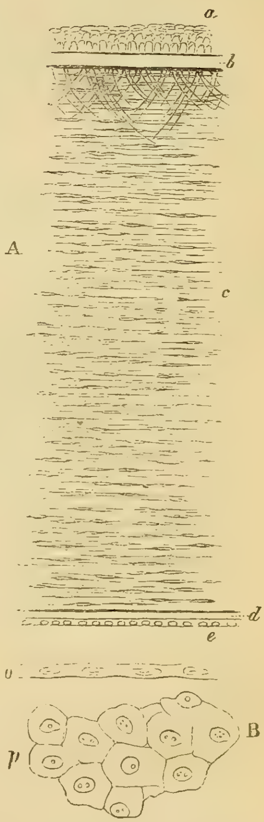
Fig. 110.



Tubes of the Cornea Proper, as shown in the eye of the Ox by mercurial injection.—Slightly magnified.

ture, passing from one to the other, and making it impossible to trace any one lamella over even a small portion of the cornea. The resulting areolæ, which in the sclerotic are irregular, and on all sides open, are converted in the cornea into tubular spaces, which have a very singular arrangement, hitherto undescribed. They lie in superposed planes, the contiguous one of the same plane being for the most part parallel, but crossing those of the neighbouring planes at an angle, and seldom communicating with them (fig. 110). The arrangement and size of these tubes can be shown by driving mercury, or coloured size, or air into a small puncture made in the cornea. They may also be shown under a high power by moistening a thin section of a dried cornea, and opening it out by needles. The tissue forming the parietes of these tubes is membranous rather than fibrous, though with the best glasses a fibrous striation may be frequently seen, both in the laminæ separating the different series of tubes, and in that dividing those of the same layer from each other. By acetic acid, also, the structure swells, and displays corpuscles resembling those apparent in the white fibrous tissue. Such is the lamellar structure of the cornea, which makes it so much easier to thrust an instrument horizontally than vertically into its substance. The tubes or elongated spaces of which we have spoken, are not distended with any fluid, but are merely moistened in the same way as the areolæ of ordinary areolar tissue. A perfectly fresh and transparent cornea is rendered opaque by pressure, but it regains its brilliance on the removal of the compressing force. Some have supposed this to result from the expulsion of fluid from between its laminæ; but that the opacity is owing simply to a derangement of the elementary parts of its structure is plain from the fact, that the same phenomena are exhi-

Fig. 111.



A. Vertical section of the Human Cornea. *a.* Conjunctival epithelium. *b.* Anterior elastic lamina, from which there pass off a number of fibres into *c*, the layers of the cornea proper, among which the nuclei are apparent. *d.* Posterior elastic lamina. *e.* Posterior epithelium.—Magn. 80 diam.

B. The posterior epithelium, *o*, seen in section; *p*, seen in face.—Magnified 300 diameters.

bited by a section however thin, immersed in water, and deranged by stretching.

Of the anterior elastic lamina. — This is a transparent, homogeneous lamina, co-extensive with the front of the cornea, and forming the anterior boundary of the cornea proper. It is a peculiar tissue, the office of which seems to be that of maintaining the exact curvature of the front of the cornea; for there pass from all parts of its posterior surface, and in particular from its edge, into the substance of the cornea proper and sclerotic, a multitude of filamentous cords, which take hold, in a very beautiful artificial manner, of the fibres and membranes of those parts, and serve to brace them and hold them in their right configuration (fig. 111, *b*). These cords, like the elastic lamina of which they are productions, appear to be allied to the yellow element of the areolar tissue. They are unaffected by the acids. The anterior elastic lamina sustains the conjunctival epithelium which covers the cornea, and is very probably the representative of the basement membrane of the mucous system, as it occupies the corresponding position in regard to the epithelium. Its thickness is about $\frac{1}{2000}$ of an inch.

The *conjunctival epithelium* of the cornea may always be obtained from a fresh eye, by gently scraping its surface. It consists of three or four layers of superposed particles, inclining to the columnar form where they rest on the anterior elastic lamina, and becoming imbricated scales on the surface (fig. 111, *a*). In many of the larger animals this epithelium consists of a much deeper series of nucleated particles, and its transparency then becomes a remarkable character.

It is in this epithelium that particles driven with force against the eye generally lodge, and it is easily detached by the instrument used to extract them. Vessels shooting into the cornea in disease lie under it, and small ulcers are formed by its destruction. In animals which cast their skin this lamina is shed with the cuticle of the body.

The *posterior elastic lamina* of the cornea (fig. 111, *d*) is a very thin membrane in which no structure can be detected. It has all the transparency of glass, and does not become opaque by maceration, boiling, or the action of acids. It adheres but slightly to the cornea proper, and, when peeled off, it has such a tendency to curl with its anterior surface inwards, that it is difficult to retain a piece of it in an extended form. If floated in water, it exhibits a peculiar glistening lustre resulting from its density. It readily tears, yet is so hard that it is bitten through with difficulty. Its elasticity is great, and has been supposed to contribute to

the exact maintenance of the curvature of the cornea, so necessary for correct vision. This lamina extends only to the circumference of the cornea, where it becomes thinner; and it ceases at the border of the iris, in a manner hereafter to be described.

Of the epithelium of the aqueous humor.—The elastic lamina is itself lined by an exceedingly delicate epithelium, which exactly resembles that existing on serous membranes, (fig. 111, *e*, *o*, *p*; see also p. 129, vol. i.) This epithelium is probably concerned in the secretion of the aqueous humor, but it does not extend over the whole surface with which that fluid is in contact. It is probably limited to the cornea.

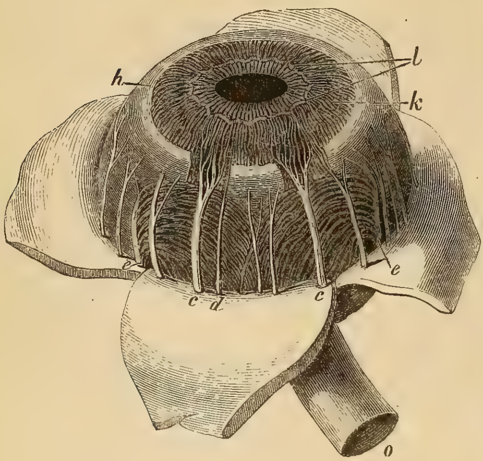
Of the Choroid.—On turning aside the sclerotic and cornea (fig. 112), the choroid, with its process the iris, is exposed. The choroid is of course perforated behind by the optic nerve. Around this it adheres pretty firmly to the sclerotic, but in the rest of its extent very slightly, and only by the medium of a slender web (*lamina fusca*), and of those vessels and nerves which pass from the one coat to the other. The rupture of these adhesions occasions a flocculent appearance of the choroid, and sets free some of the brown colouring matter with which its structure is loaded. There is no serous cavity between the sclerotic and choroid, as some have imagined, for a true epithelium is wanting, though the lamina fusca contains nuclei.

The choroid, on coming up to the cornea, gives off its process the iris, and it there adheres intimately to the sclerotic by a very narrow ring of white tissue—the ciliary ligament. For an eighth of an inch behind this, however, it is coated by a semi-transparent band, which we shall distinguish as the ciliary muscle, and the fibres of which radiate from the cornea.

The *choroid* contains some fibrous tissue, resembling that of the sclerotic; but it is composed principally of blood-vessels and pigment-cells. It has been usual to describe it as having two layers, an arterial and a venous; an incorrect view. It is in fact essentially a thin lamina of capillaries, disposed in a close network, the meshes of which are rather smaller behind than in front. This plexus forms the inner surface of the choroid, and has been known as the *tunica Ruyschiana.* The arteries supplying it, and the veins carrying off its blood, come to it and leave it at very numerous points, but on its outer surface only, where they are so thickly arranged, side by side, as to appear to form the whole of that surface. The veins in particular are large and numerous, and disposed in beautiful curves, converging to four or five trunks, before quitting the choroid, and

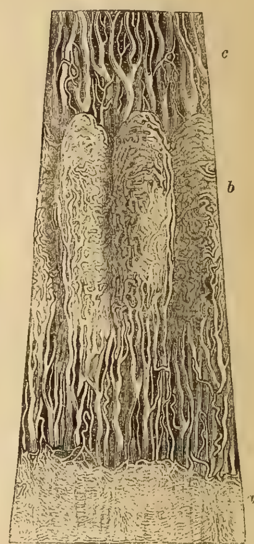
styled the *vasa vorticosa* (fig. 112, *e*, *e*). The arteries run between these, but less regularly.

Fig. 112.



Choroid and Iris, exposed by turning aside the sclerotica:—*c*, *c*. Ciliary nerves branching in the iris. *d*. Smaller ciliary nerve. *e*, *e* Vasa vorticosa. *h*. Ciliary ligament and muscle. *k*. Converging fibres of the greater circle of the iris. *l*. Looped and knotted form of these near the pupil, with the converging fibres of the lesser circle of the iris within them. *o*. The optic nerve.—From Zinn.

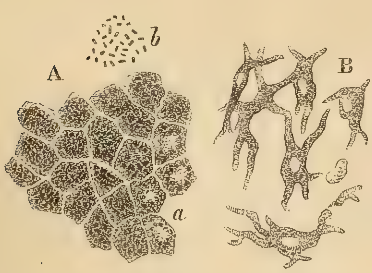
Fig. 113.



Vessels of the Choroid, Ciliary processes and Iris, inner surface. —*a*. Portion of the capillary network or *tunica Ruyschiana*. *b*. Ciliary processes. *c*. Portion of the iris.—From an Infant. Magnified 14 diam. After Arnold.

The capillary network of the inner surface is so close that there is no room for pigment-cells in its interstices; but between it and the arteries and veins, as well as among the veins themselves, there is a great abundance of colouring matter, which deeply tinges the whole thickness of the membrane.

Fig. 114.



A. Choroidal Epithelium, with the cells filled with pigment, except at *a*, where the nuclei are visible. The irregularity of the pigment-cells is seen. *b*. Grains of pigment.
B. Pigment-cells from the substance of the Choroid. A detached nucleus is seen.—Magnified 320 diameters.

The pigment-cells in the substance of the choroid (fig. 114, B) are extremely irregular in shape, and lie in various directions amongst the other elementary tissues. Similar ones are found in the iris, and sparingly in the anterior part of the sclerotic. They are so loaded with pigment that their nuclei are often obscured by it.

The pigmentary matter within these cells is of a sepia colour, and occurs in the form of oblong or oval grains, less than $\frac{1}{10000}$ of an inch long (fig. 114, *b*). These grains exhibit molecular motion when removed from the cells, and sometimes even within the cells (vol. i. p. 60). They are insoluble in hot or cold water, in the dilute mineral acids, and in strong acetic acid, in oil, alcohol, and ether; but are dissolved, after long digestion, by diluted liquor potassæ. The ash consists of common salt, lime, phosphate of lime, and oxide of iron (*Gmelin and Berzelius*).

In albinos the colouring matter is deficient, not only in the eyes, but in other organs in which it usually exists. The eyes have consequently a pink appearance, derived chiefly from the blood in the choroid and iris.

Of the Choroidal Epithelium.—On the inner surface of the choroid, within the capillary network, and adhering slightly to it, is an epithelium, consisting of a single layer of nucleated particles, of a pentagonal or hexagonal shape, filled with pigment. This was first particularly described by Mr. Wharton Jones, who termed it the *membrane of the black pigment.* In using this name, it must be remembered that the colouring matter is not peculiar to this epithelium; and that this epithelium exists without pigment in front of the tapetum lucidum of animals; and also that it is present, without pigment, in albinos, as was first pointed out by Mr. Jones. Hence the presence of pigment in its cells is a secondary character. The nuclei of the cells project on the inner surface of the membrane. They are concealed by the pigment if it is very abundant, but in general they are visible. Both conditions are seen in fig. 114, A.

In many quadrupeds and fishes the inner surface of the choroid, in its posterior part, has a brilliant lustre, owing to the presence of a thick layer of wavy fibrous tissue, peculiarly arranged, outside the choroidal epithelium (here colourless). This *tapetum lucidum* must act as a concave reflector, causing the rays of light to traverse the retina a second time, and thus, probably, increasing the visual power, particularly when the quantity of light admitted into the eye is small.

In the osseous fishes there is a singular vascular organ of a horse-shoe shape appended to the outer surface of the choroid, and covered by a silvery membrane. Its structure is imperfectly made out, and its office is quite unknown. It is called the *choroid gland.*

In birds there is a remarkable plicated, comb-like process of the choroid, projected into the vitreous humor, and termed the *pecten.* It is a vascular membrane, and covered with pigment; its base commencing at the entrance of the optic nerve, and its apex reaching more or less nearly to the crystalline lens. The retina does not extend over it. No satisfactory use has yet been assigned to it. Its size and shape are subject to considerable variety.

The description of the choroid now given refers only to that portion of it which corresponds to the retina, and this latter membrane ceases at a line (*ora serrata*) about an eighth of an inch behind the margin of the cornea. In front of this line, and as far as the iris, the choroid is known as the *ciliary body*, being modified to form the *ciliary processes;* and it is covered on its outer surface by a semi-transparent tissue, the *ciliary muscle*, at the anterior edge of which is a more opaque white ring, the *ciliary ligament.*

The *ciliary processes of the choroid* project as folds, or plaitings, into the vitreous humor, and are there lodged in corresponding folds, the *ciliary processes of the vitreous body.* They are seen from within to commence at the anterior border of the retina, or *ora serrata*, as mere streaks, converging towards the lens; and it is only when advanced more than halfway to that body that they become projected into about sixty or seventy plaits, with subordinate ones between. These terminate by small free extremities, which slightly overlap in front the border of the lens, without touching it, being united to it through the medium of a delicate layer of the hyaloid membrane of the vitreous humor. These folds take firm hold of the vitreous humor in its front part, all round the lens. Their texture is very vascular (fig. 113, *b*) and filled with irregular pigment-cells, (which in the human eye are least numerous on the most prominent parts,) and on their inner surface is a tough colourless lamina, composed of ill-defined nucleated cells, (continuous with the border of the retina, but clearly not composed of nervous matter,) by means of which they are immediately connected with the hyaloid membrane. The strength of this connexion is evinced in attempts to sever it in the recent eye. After a certain amount of decomposition has taken place, the separation is much more easy. The ciliary processes by their anterior surface, near their apex, contribute to form the posterior wall and side of the posterior chamber, and are continuous with the back of the iris. They are there free, and washed by the aqueous humor. The ciliary processes are covered, and therefore concealed, on the outside by the ciliary muscle.

The *iris* may rightly be regarded as a process of the choroid; it is continuous with it, although of a modified structure. It forms a vertical curtain stretched in the aqueous humor before the lens, and perforated for the transmission of light. It is attached all round at the junction of the sclerotic and the cornea, so near indeed to the latter that its anterior surface becomes continuous in the following manner with the posterior elastic lamina. This lamina near its

border begins to send off from its anterior surface, or that towards the laminated cornea, a network of elastic fibres, which stretch towards the border, becoming thicker as they advance, until at length the entire thickness of the lamina is expended by being converted into them. These fibres then bend backwards from the whole circumference of the cornea, to the circumference of the front of the iris, and are there implanted, passing in this course across the rim of the anterior chamber, and through the aqueous humor. They are seen more easily in some animals than in others, forming a regular series of pillars around the anterior chamber. Behind these there is a more diffused union of the tissue of the iris with the sclerotic, by means of the ciliary ligament. The iris is continuous behind, near its border, with the ciliary processes, and is only free in the inner half of its extent, near the pupil, where it is covered with a dense layer of pigment, and marked by converging striæ. This posterior surface is termed *uvea*. In consequence of the extreme proximity of the iris to the lens, the posterior chamber is much less capacious than the anterior, as it is likewise of smaller diameter.

Fig. 115.

Network of yellow fibrous tissue at the border of the elastic lamina of the cornea:—*a*. Outer border, where the fibres approach the iris. At their inner end, *b*, they are lost on the elastic lamina.—Magnified 70 diameters.

The anterior surface of the iris has a brilliant lustre, and is marked by lines accurately described by Dr. Jacob, taking a more or less direct course towards the pupil. These lines are important as being indicative of a fibrous structure. Slender, and very numerous in the outer three-fourths of the membrane (the pupil being contracted), and often crossed near the border by wave-like differently coloured lines, they unite at about $\frac{1}{12}$ of an inch from the pupil into a circular series of knotted and much thicker elevations, from which finally proceed a multitude of minute branching and anastomosing filaments, to the extreme verge of the pupil. When the pupil is contracted, these converging fibres are stretched; when it is dilated they are thrown more or less into zigzags. The pupil is nearly circular, and is situated rather to the inner side of the centre of the iris. By the movements of the iris it is dilated or contracted, so as to admit more or less light to the interior; and its diameter under these circumstances may vary from about $\frac{1}{20}$ to $\frac{1}{3}$ of an inch.

The varieties of colour in the eyes of different animals and individuals depend almost solely on the colour of the front of the iris, which itself resides chiefly in pigment-cells, situated in its substance rather than as a layer on its anterior surface. These cells are most irregular in shape and size, and lie in the interstices of the more essential tissues, which they much obscure. The iris is consequently best examined in albino specimens.

The iris is undoubtedly contractile, and the anatomical characters of its principal tissue so nearly resemble those of unstriped muscle, that it may be considered as a variety of that tissue. Its fibres are loaded with nuclei which are rather rounder than those of unstriped muscle, and more loosely attached to the contractile material. The principal direction taken by the fibres is towards the pupil, although they are more or less meandering and interlacing in this course. Arrived near the pupil, they appear to join, and form indistinct arches. In many instances it is easy to detect a set of circular fibres, either gathered into a principal bundle near the pupil or more diffused, but always lying in front of the others. These seem to answer to the circular fibres of the bird's iris, which are of the striped variety, and occupy the front of the membrane. There may also be usually distinguished in the very thin margin of the pupil an arrangement of fibres more circular than radiating.

The iris is so vascular that some anatomists have considered it erectile, and have erroneously ascribed its movements to this property. But its vessels are slender and delicate, and resemble those of the unstriped muscle. They are derived chiefly from the two long ciliary arteries, which on approaching it bifurcate, and form a circle around it, whence pass inwards a great number of minute branches, which form loops near the pupillary margin.

On the anterior surface near the pupil a vascular circle marks the line from which in the fœtus the *membrana pupillaris* stretched across in front of the pupil. This membrane at that early period divides the anterior from the posterior chamber and receives from several parts of the circular vessel last mentioned, small branches which approach the centre, and then return in arches, after inosculating sparingly across the central point. The membrana pupillaris is almost absorbed at birth.

The grayish structure coating the choroid for about an eighth of an inch behind the cornea, presents at its anterior edge a more white and opaque circle, the *ciliary ligament*, which seems to be chiefly of a fibrous character, and to connect the border of the

iris firmly to the sclerotic. The plexiform tissue of the posterior elastic lamina of the cornea already noticed, adjoins this ligament, and partially blends with it.

The *ciliary muscle* is that grayish, semi-transparent structure behind the ciliary ligament, and covering the outside of the ciliary body. It has been described as muscular by many of the older anatomists, especially by Porterfield, while others have assigned to it a different character. Lately it has been so regarded by Wagner and Dr. Wallace of New York, and we believe correctly. It belongs to the unstriped variety of muscle, and its fibres appear to radiate backwards from the junction of the sclerotic and cornea, and to lose themselves on the outer surface of the ciliary body. The more superficial fibres are in contact with, but scarcely adhere to, the sclerotic, and are inserted into the posterior part of the ciliary body; while the deeper ones seem to dip behind the iris to the more prominent parts of the ciliary processes which approach the lens. The ciliary muscle must have the effect of advancing the ciliary processes, and with them the lens, towards the cornea. The ciliary nerves pierce this muscle on their way to the iris, distributing to it many filaments which may be seen for the most part to cross the fibres.

Fig. 116.

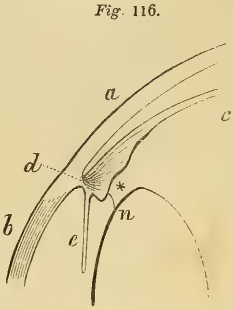


Diagram to show the position and action of the Ciliary Muscle:—*a*. Sclerotic. *b*. Cornea. *c*. Choroid, separated a little from the sclerotic. *d*. Situation of the ciliary ligament, and point from which the ciliary muscle radiates. *e*. Iris. *n*. Lens, connected with the ciliary processes by the anterior wall of the canal of Petit, the situation of which is marked by the *.—Magnified 3 diameters.

The muscular nature of this structure is confirmed by its anatomy in birds, where it is largely developed, as noticed by Sir P. Crampton. We find its fibres to be of the striped variety, like the circular fibres of the iris in the same class, and to be supplied by ciliary nerves traversing the muscle in a circular direction. They likewise all radiate from the cornea, at the circumference of which they are attached to the deeper layers of the cornea proper, the elastic lamina being here exceedingly thin.

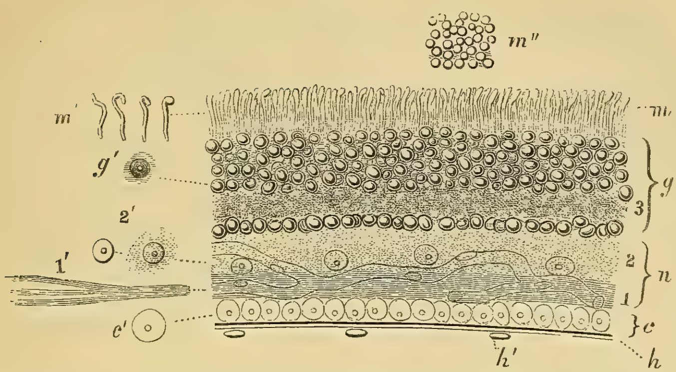
Within the choroid is the retina, which we shall describe as a structure distinct from the optic nerve, though continuous with it; reserving our account of that nerve, and of the others pertaining to the eye, till the anatomy of the globe is concluded.

The *retina* is the sheet of nervous matter which receives the images of external objects thrown upon it by the transparent media, and it is accordingly placed immediately behind the vitreous hu-

mor, the deepest of those media. It may be said to commence at the foramen in the sclerotic and choroid by which the optic nerve enters the eye, and to terminate by a finely jagged border (the *ora serrata*) at the hinder border of the striated part of the ciliary body. It is thicker behind, in the deepest part of the globe, and gradually thinner forwards. Of a pinkish gray tint, and semi-transparent when fresh, the images formed upon it may be seen through it from behind, if the sclerotic and choroid coats be first carefully removed. When thrown into accidental folds, it resembles in appearance the vascular gray substance of the cerebral convolutions. The exquisite function performed by this nervous membrane, its expanded form and separability from other structures, have always made it an object of peculiar interest with physiologists, who have not unreasonably expected that important secrets of nervous function might be disclosed by an accurate insight into its structure. Whatever the conclusions to be drawn, it is certain that this structure is elaborate and complex, and worthy of an attentive study.

The first part of the retina to be described is the *fibrous gray layer*, which forms the immediate continuation of the optic nerve, and which is seated on its inner surface. This is a layer of fibrous character, radiating from the end of the optic nerve, and apparently consisting of the tubular fibres of that nerve deprived of their white substance ; that is, being no longer tubular and white, but solid and gray, and united together more or less into a membrane. This at least seems to us to be certain, that the white substance of Schwann does not exist in the nervous substance of the retina, but ceases as the nerve perforates the sclerotic. It has been particularly described as existing in the retina of the rabbit ; but the fact seems to be, that in this animal the nerve does not end in the retina till some way within the globe, for, after bifurcating and spreading out as a white streak within the choroid, the bundles of nerve-tubes suddenly lose their white lustre, and assume the appearance of the gray fibres of the layer now under consideration. These bundles, both in animals and man, may be seen to anastomose in a close plexiform manner, especially near the optic nerve, and finally constitute a thin sheet, which becomes thinner and less fibrous as we trace it forwards, until at length it can be no longer discerned. This fibrous gray layer of the retina is united to the hyaloid membrane, containing the vitreous humor, by a layer of nucleated cells almost perfectly transparent, and sometimes very difficult of discovery on that account. It is to be remarked, that the fibrous gray layer is

Fig. 117.



Vertical section of the Human Retina and Hyaloid Membrane. *h*. Hyaloid membrane. *h'*. Nuclei on its inner surface. *c*. Layer of transparent cells, connecting the hyaloid and retina. *c'*. Separate cell enlarged by imbibition of water. *n*. Gray nervous layer, with its capillaries. 1. Its fibrous lamina. 2. Its vesicular lamina. 1'. Shred of fibrous lamina detached. 2'. Vesicle and nucleus detached. *g*. Granular layer. 3. Light lamina frequently seen. *g'*. Detached nucleated particle of the granular layer. *m*. Jacob's membrane. *m'*. Appearances of its particles, when detached. *m''*. Its outer surface.—Magnified 320 diameters.

the only nervous element of the retina existing over the extremity of the optic nerve where it enters the globe—a spot incapable of vision. Immediately around this spot, the other layers commence which have now to be described, and the first of these is the *vesicular gray layer*. This layer is on the outer surface of the fibrous layer, and so intimately blended with it, that it might almost seem as if the fibres successively terminated in it. The vesicular layer is thicker behind, and gradually thinner forwards. It very accurately corresponds with the vesicular matter of the convolutions of the cerebrum, consisting of a finely granular matrix with interspersed very delicate vesicles, furnished with pellucid globular nuclei of characteristic appearance.

The blood-vessels of the retina, which are thickly distributed, belong solely to the fibrous and vesicular layers now mentioned. The central artery of the retina, after entering the globe in the axis of the optic nerve, sends four or five radiating branches, which almost immediately perforate the fibrous layer and spread out in a beautifully arborescent manner, as a capillary network in the substance of the vesicular stratum. After slight maceration, it is easy to wash the nervous material out of the meshes of the vessels; and they then form a vascular layer, but which it is hardly correct to describe as a distinct lamina of the retina. They are merely the nutrient vessels of the part, and are the representative of the close network of the gray substance of the cerebral convolutions. Their

wall is a diaphanous membrane with nuclei projecting at intervals, and the meshes average $\frac{1}{400}$ of an inch diameter.

Behind the vesicular gray layer is the *granular layer*, a term we shall apply to it, because it seems to consist of a close aggregation of small granules, which refract the light more powerfully than the neighbouring parts, and have scarcely any appearance of intervening matrix; they might be regarded perhaps as analogous to the nuclei of cells, and much resemble a layer of granules in the substance of some of the cerebral convolutions, and of the laminæ of the cerebellum. They are made more evident by acetic acid. This layer is divided into two, of which the inner is much the narrower, by a *pale stratum*, which can only be seen by very careful manipulation.

On the outside of the granular layer is that remarkable lamina, known by the name of its discoverer, the *membrana Jacobi*. It consists of club-shaped rods, placed uprightly, the thin end inwards, the thick outwards; and it is very easily detached from the rest of the retina, when the choroid is removed, so as to float as delicate shreds, visible to the naked eye, in the water in which the eye is immersed. The rods have a tendency to separate from one another when placed in water, and the club-shaped extremities are then often seen to be formed by a sudden bending back of the stem like a crook, which may be more or less opened out. Interspersed among the rods are seen on the outer surface a number of clear spaces, as though transparent cells were disseminated among them. This layer forms the connecting medium between the retina and the choroidal epithelium.

Fig. 118.

Outer surface of the Retina, showing the membrane of Jacob, partially detached.—After Jacob.

It has been before stated that the optic nerve pierces the sclerotic and joins the retina about an eighth of an inch on the inner side of the axis of the eye. Precisely in this axis, the retina is of a decidedly yellow colour in a roundish spot of about $\frac{1}{24}$ of an inch diameter, called, after its discoverer, the *yellow spot of Sœmmerring*. This spot exists only in man and the monkey among mammalia, but an analogous part has been found by Dr. Knox in reptiles. It has been described by some as a fold, by others as a foramen in the retina, and after several examinations we should speak of it as a small

mound, or projection of the retina towards the vitreous humor, with a minute aperture in the summit. On removing the sclerotic and choroid with the utmost care, the interior of the globe can be seen from the outside, through this hole; and yet the membrane of Jacob appears to be continued over it. On examining the structure of the retina about the yellow spot, from within, the fibrous expansion of the optic nerve (though stretching in every other direction to a much greater distance) cannot be traced quite up to the spot itself. Nucleated cells occupy the elongated meshes of the fibrous plexus already described, until at length the fibres disappear, and the closely set cells seem to cover the whole surface of the spot. The gradual subsidence of the fibres in the interstices of the cells we have distinctly seen. As for the colouring matter, it is not in grains of pigment, but stains the several tissues, and soon disappears in water. The use of the yellow spot is unknown. It is interesting to observe in connection with the perfection of vision over the spot, that the principal branches of the artery and vein of the retina, above and below, curve round it at a distance, going, as it were, out of their course to avoid it, so that only capillary vessels are found in its immediate vicinity.

Fig. 119.

The yellow spot of the Retina occupying the axis of the eye; and the entrance of the optic nerve, with the arteria centralis retinæ on the inner side of the axis.—After Sœmmerring.

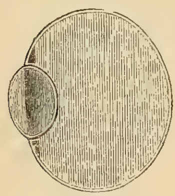
It now remains to describe the transparent media which occupy the interior of the ball of the eye.

The *vitreous body*, lying in the concavity of the retina, and filling all but about the anterior fifth of the globe, has, when entire, the consistence of soft jelly. It consists of an exceedingly fine and close, but perfectly transparent web of fibrous tissue, the meshes of which are exceedingly small, and contain an aqueous fluid. If the tissue be cut into, the water will slowly drain off, showing the continuity of the cells with one another; and the manner in which they are constructed by interlacing fibres may be very plainly seen with a high power near the ciliary processes, in the vicinity of which these fibres are particularly strong. The whole vitreous body is bounded by or contained in an envelope of extremely thin homogeneous membrane, having corpuscles or cell-nuclei on its inner surface, where the fibrous tissue is attached (fig. 117, h, h'). It would perhaps be convenient to restrict the term *hyaloid membrane* to this envelope. Where the retina extends, that is, as far as the ciliary body, the hyaloid membrane is in contact with its inner surface, and united

to it by an extremely *transparent layer of cells*, which often remain invisible until swollen by the imbibition of water (fig. 117, *c*, *c′*). These cells serve merely as a bond of connexion between the hyaloid membrane and the fibrous lamina of the retina. Between the anterior border of the retina and the border of the lens, the vitreous body is accurately adapted to the ciliary striæ and processes of the choroid, and presents a series of plaitings precisely similar to those of the processes themselves, and termed the *ciliary processes of the vitreous body*. Collectively they form a circle called *zonula ciliaris*, or, *zone of Zinn*. The two structures are in a manner dovetailed into one another; and so intimate is their union, that, when the processes of the choroid are drawn away from the vitreous body, some of their pigment is generally left adhering to the processes of the latter.

In the centre of its anterior surface, in a space nearly corresponding to the area between the points of the ciliary processes, the vitreous body is hollowed out to receive the crystalline lens. This latter is contained in, or bounded by, a perfectly closed capsule, composed of a tissue exactly resembling the elastic lamina of the cornea already described. To the whole posterior surface of this capsule, and to a very narrow circumferential portion of its anterior surface, the fibrous structure of the vitreous body is firmly attached; the hyaloid membrane itself not passing behind the lens, but adhering to the capsule all round a little in front of its rim, after crossing the interval separating the tips of the ciliary processes of the choroid from the lens. Thus the rim of the lens is not exactly at the surface of the vitreous body, but buried slightly within it, and overlapped a little by it. All round the rim of the lens, there is a cavity in the vitreous body, extending under the circle of the ciliary processes of the latter, and termed the *canal of Petit* (fig. 120, and fig. 116*). The hyaloid membrane constituting these ciliary processes forms the anterior wall of this canal, which, by its adhesion to the ciliary processes of the choroid, is subject to be drawn forwards by the contraction of the ciliary muscle already described (p. 27). When this occurs, the lens also is advanced, in consequence of the union of this anterior wall of the hyaloid to its anterior surface near the rim. Were the canal of Petit wanting, the ciliary muscle

Fig. 120.



Position of the Lens in the vitreous humour, shown by an imaginary section. The dark triangular space on each side of the lens is intended to indicate the position of the canal of Petit.—After Arnold.

would act rather on the vitreous body around the lens, than on the lens itself. Its existence may be easily shown by filling it with mercury or air, through an artificial orifice in its anterior wall. The injected fluid fills out the plaitings of the ciliary processes.

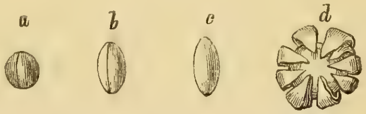
The refracting index of the vitreous body is about 1·339, that of water being 1·336, so that the difference between them is very trifling, and may be referred in part to the transparent fibrous tissue. Its chemical constitution, according to Berzelius, is as follows:

Water	98·40
Chloride of Sodium, with extractive matter .	1·42
Albumen	·18
	100·00

In early life the vitreous body gives passage by a canal to a branch of the central artery of the retina to the back of the lens; and in large animals, though not in man, this appears to supply some branches to the vitreous body itself even in the adult state.

The *crystalline*, as already mentioned, is a double convex lens; but its surfaces are of unequal curvature, the posterior being the more convex. In the adult the difference is nearly as 4 to 3, but it is liable to some variety in different subjects. Chossat has observed that the curvatures of the lens in the ox are ellipsoids of revolution round the lesser axis, but whether they are so in man is not determined: the subject is one very difficult of investigation. The lens alters its shape with age; being in the fœtus more spherical, more flattened in childhood, and still more so in advanced life. In infancy it projects into the aqueous humor so as to touch the iris; but in old age there is a space intervening. The lens also varies in consistence with age; being very soft at an early period, very firm in declining years. At no epoch of life, however, is it of uniform consistence throughout; being always denser and firmer from without inwards. In the adult its diameter is from $\frac{1}{3}$ to $\frac{3}{8}$ of an inch, and its antero-posterior axis about $\frac{1}{8}$ to $\frac{1}{6}$ of an inch. It weighs from three to four grains.

Fig. 121.



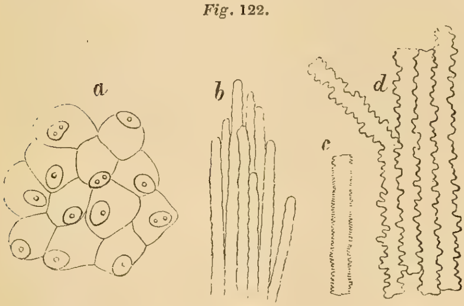
Human Lens:—*a.* At birth. *b.* At six years old. *c.* Adult. *d.* Hardened in spirit, and partially separated into segments.—After Sœmmerring.

The lens is divided into *capsule* and *body*. The manner in which it is encased and fixed by the capsule in the vitreous body, has been

already described. It only remains to add, that the anterior wall of the capsule is nearly four times thicker than the posterior; greater strength being required in front, where the surface is free in the aqueous humor, than behind, where it is adherent to the tissue of the vitreous body. The diminution in thickness does not occur abruptly at the rim of the lens, but commences gradually on the anterior surface near the rim, at a line corresponding to the attachment of the anterior wall of the canal of Petit. The capsule is perfectly closed, and cannot allow of the passage of either vessel or nerve to its interior.

The *body* of the lens is constructed in a manner calculated to excite admiration. Its superficies, by which it comes into contact with the capsule, consists of a layer of extremely transparent nucleated cells represented in fig. 122, *a*. These cells form an organized connecting medium between the body and capsule of the lens, and there is no interspace not occupied by them. After death they very soon become loaded with water (absorbed most probably by the capsule from the aqueous humor), which is the *aqua Morgagni*, that some have supposed to exist naturally between the capsule and body of the lens near its border.

Fig. 122.

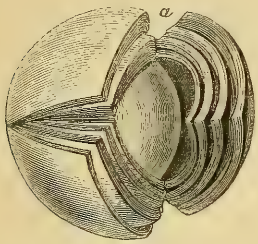


a. Cells connecting the body of the lens to its capsule (human). *b*. Fibres of the lens, with slightly sinuous edges (human). *c*. Ditto from the Ox, with finely serrated edges. *d*. Ditto from the Cod; the teeth much coarser.—Magnified 320 diameters.

The body of the lens is composed of fibres superimposed on one another, and united side to side in laminæ, of which many hundreds must exist. The mode of arrangement of the fibres is, however, more artificial than this. In the mammalia in general there are visible on the front surface, when the lens has slightly lost its transparency, three lines, extending from the centre two-thirds to the border, and dividing it into three equal parts: and on the opposite surface three similar lines exist, having an intermediate position. From and to these lines the fibres pass from surface to surface. Thus, a fibre proceeds from the centre in front, advances midway between two of the lines over the border, and comes on the opposite surface to the extremity of one of the lines. Others pass from the extremities of the lines in front, and are lost in the centre

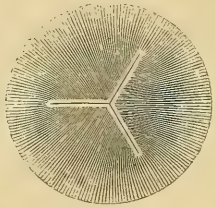
behind. And the rest of the superficial plane are intermediate to these, and as nearly parallel as their curved course will allow. If we

Fig. 123.



Lens, hardened in spirit and partially divided along the three interior planes, as well as into lamellæ.—Magnified 3½ diameters. After Arnold.

Fig. 124.



Triple line on the surface of the Lens of the Sheep, with the radiation of the fibres indicated. The interspace between the radiating lines at the circumferences of this figure would each include about a hundred fibres.—Magnified 3 diameters.

now consider that these lines on the surface are but the edges of planes which dip to the centre, and afford points of divergence and concourse for all the fibres deep as well as superficial, we shall readily comprehend what may at first sight seem an intricate structure. This arrangement was known to Leeuwenhoeck, and has been shown by Sir D. Brewster to present varieties in different classes of animals. In the human lens we find the tripartite division is seen imperfectly, and only in the centre; for the three primary diverging lines bifurcate again and again, and with considerable irregularity, so that the ultimate subdivision is into from twelve to sixteen parts in the adult, but only from four to six in the fœtus.

To the account now given may be added, that as the fibres are shorter in proportion as they are more internal, so do they appear narrower, more cylindrical, solid, and intimately united to each other, as we trace the structure inwards. The superficial fibres are flattened according to the surface they answer to; and of all it may be said, that they are narrower towards their extremities, as their arrangement renders necessary. The edges of the fibres in fishes are most beautifully toothed, and dovetailed together, as Sir D. Brewster pointed out (fig. 122, *d*); and something similar may be detected in the more superficial fibres of the lens of the larger mammalia, and in man. But the deepest fibres present scarcely any trace of this elegant structure. Near the tripartite division of the lens the fibres are more united than elsewhere, and appear more or less consolidated together. The average thickness of the fibres in man is about $\frac{1}{5000}$ of an inch.

The increasing density of the lens towards its centre is attended with an increase of the refracting power, designed to augment the convergence of the central rays of the transmitted pencils in their course through the lens, and thus to bring them to the same focus with the circumferential rays. Sir D. Brewster states the refracting power of the lens at its surface to be 1·3767, and at the centre 1·3990.

The lens, during its development, has a very copious distribution of blood to the outer surface of its capsule, from two sources. The central artery of the retina sends a vessel through the vitreous humor to the centre of its posterior surface, which branches into a radiating series of capillaries investing it as far as the border, where they anastomose with vessels derived from the ciliary processes, which proceed some way over the front of the capsule, and return in loops. None of these vessels continue after the lens has attained to maturity.

The lens consists chiefly of albumen, and becomes hard and opaque by boiling. The central parts evidently contain a smaller proportion of water than the outer layers, which merely become flocculent by the action of heat. The fibrous and lamellar structure is more easily seen when thus rendered opaque, and it then separates more easily along the triple or multiple planes already indicated. Berzelius states the precise chemical constitution of the lens to be as follows:

Water	58·
Albumen	35·9
Alcoholic extract, with salts	2·4
Watery extract	1·3
Membrane	2·4
	100·0

The *aqueous humor*, as its name imports, is very nearly pure water, containing, according to Berzelius, less than a fiftieth of its weight of other matters, of which more than half is chloride of sodium, and the rest extractive, soluble either in water or alcohol.

It fills up the space between the cornea and lens—a space divided into two cavities by the membrana pupillaris in the fœtus, and still partially divided by the iris into an *anterior* and *posterior chamber*, continuous through the pupil. The anterior, though small, is much larger than the posterior, and is bounded by the cornea in front, the iris behind, and a portion of the ciliary ligament at its circumference. The posterior is bounded by the iris in front, the lens and

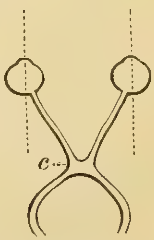
a narrow circle of hyaloid membrane behind, as well as by the ciliary processes which slope towards the iris, and thus limit the lateral dimensions of the chamber. It is very easy to imagine the existence of a lining membrane to this cavity of the aqueous humor, such as would form a closed sac, and answer to the serous structures; and a *membrane of the aqueous humor* has accordingly been described by several anatomists. But the most careful observation fails to detect any such *serous sac*, though the posterior epithelium of the cornea (p. 21) closely resembles that of serous surfaces. No epithelium exists in front of the iris, and certainly none is present on the anterior surface of the lens: this we can aver from repeated examination. On the posterior surface of the iris, however, there seems to be a pigmentary membrane.

Of the Optic Nerves, and their central connexions.—The second pair of nerves is devoted to the sense of sight, and on that account has received the name of Optic Nerves.

The marked manner in which these nerves terminate in the retinæ, the constant relation in size between them and the organ of vision, the atrophy which they suffer when the visual apparatus has been destroyed, the impairment or loss of vision which follows a morbid state of them, place it beyond all question that they are the proper conductors of visual impressions to the sensorium.

The optic nerves form a most extensive connexion with the brain through the *optic tracts*. The optic tracts are two flattened bands of nervous matter, which proceed from the posterior and superior surface of the mesocephale (the region of the quadrigeminal tubercles) forwards along the inferior surface of each crus cerebri, and after passing in a curved course (concave inwards) along the base of the brain, unite in front of the tuber cinereum and mammillary bodies, and form a very intimate junction, which is called the *chiasma* or commissure of the optic nerves.

Fig. 125.



Plan of the optic nerves on a small scale, showing their divergence from the chiasma, *c*, and their junction with the globe, on the inner side of the axis of the humors.

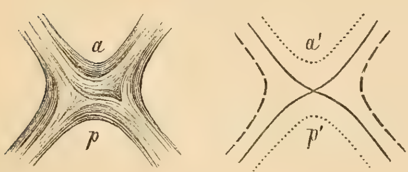
From this chiasma the optic nerves spring, and diverge as they pass forwards into the orbits through the optic foramina. This point may be looked upon, therefore, as their origin. To understand, however, more exactly their relation to the brain, it will be necessary to trace the connexions of the optic tracts, and to inquire into the structure of the chiasma.

In tracing each optic tract back from the chiasma, we find that it first forms a pretty close connexion with the locus perforatus on the

outside, and with the tuber cinereum on the inside. Whether any of its fibres spring from the tuber cinereum is matter of great uncertainty. Further back the optic tract adheres by its outer margin to the crus cerebri, and is concealed by the middle lobe of the brain. In this course it expands considerably, and at the posterior edge of the crus cerebri it forms intimate connexions with certain gangliform masses of the brain. First, we observe its connexion with the external geniculate body, a small prominent tubercle of darker colour than the surrounding parts, and situate at the posterior margin of the crus; it seems to involve the outermost fibres of the tract, as a ganglion, and from it a band of fibres is continued back to the posterior of the quadrigeminal bodies. Beneath the posterior extremity of the optic thalamus the innermost fibres of the tract form a connexion with another similar body, the internal geniculate body, from which fibres are continued backwards to the anterior of the corpora quadrigemina. The tracts thus appear to divide, each into two bands: of which the outer one, after passing through the external geniculate body, reaches the testes; and the inner one, similarly related to the internal geniculate body, reaches the nates.

The optic tracts are connected with the optic thalami chiefly *through the geniculate bodies.* Each tract adheres to the outer side of its corresponding thalamus for some distance, but whether any fibres sink into it is not determined. In the horse, dog, sheep, and monkey, this arrangement is very conspicuous, as the greater portion of the fibres of the tract expands over the internal geniculate body, which is incorporated with the posterior extremity of the thalamus. The diameter of the tubules of the optic tracts we have found to vary from $\frac{1}{1700}$ to $\frac{1}{5000}$ of an inch.

Fig. 126.



Course of fibres in the chiasma, as exhibited by tearing off the superficial bundles from a specimen hardened in spirit. *a*. Anterior fibres, commissural between the two retinæ. *p*. Posterior fibres, commissural between the thalami. *a′*, *p′*. Diagram of the preceding.

The chiasma results from the junction of the optic tracts in front of, and inferior to, the tuber cinereum. The fibres which form the inner margin of each tract, *p*, are continued across from one side of the brain to the other, and form no connexion with the optic nerves, and exist where those nerves do not exist, as in the mole. The fibres may be regarded as commissural between the thalami of opposite sides. The remaining fibres of the tracts go to form the optic nerves; the central ones pass into the

nerve of the opposite side, decussating the similar fibres of the other tract; and the outermost fibres, *much fewer* in number than the central ones, pass to the optic nerve of the same side.

This disposition of the fibres of the chiasma may be demonstrated on a specimen which has been sufficiently hardened in spirit, by tearing the fibres in their proper direction after the removal of the neurilemma. By such a procedure it may be shown that each optic nerve derives its principal fibres from the tract of the opposite side, and only a few fibres from those of its own side.

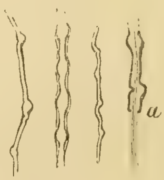
The existence of such a decussation of fibres in the chiasma is, moreover, rendered highly probable by the strong indications of most extensive decussation, resembling that of the anterior pyramids, in some of the large carnivorous birds, and also in the crossing of the entire optic nerves in some of the osseous fishes, the cod for example.

In the common domestic quadrupeds the decussation of the fibres is not to be made out so plainly, probably from its being more complicated. The chiasma somewhat resembles a knotted union of the two tracts, which is dense and firm in structure.

The optic nerves appear also to be connected by fibres, forming the anterior border of the chiasma, and which may be regarded as commissural between the two retinæ (*a*, fig. 126).

From the quadrigeminal tubercles to the chiasma, nerve-tubes, mostly of large size, are visible by the microscope in the tracts. In the chiasma and the optic nerves, the fibres, although very variable in size, are so closely connected together that it is exceedingly difficult to separate them. They seem to be collected into numerous small bundles, having an intricate plexiform interlacement within the common sheath. Each bundle is surrounded by a firm but dense neurilemma, and thus it is impossible by the ordinary means of manipulation to separate a portion of the nerve of sufficient delicacy to examine any considerable length of its fibres. The size and character of the fibres may be estimated by examining portions of them which project from the margin of the piece.

Fig. 127.



Fragments of Nerve Tubules from the human optic nerve, of various sizes, and varicose. At *a* the central axis projects beyond the white substance at a broken extremity.—Magn. 320 diam.

The optic nerve is abundantly supplied with capillaries, which form a network with elongated meshes in its substance. A little behind the globe, it receives from the ophthalmic artery a branch, before alluded to, the arteria centralis retinæ, which penetrates to

its axis, along which it runs to the interior of the eye, in a canal of fibrous tissue. This branch then radiates to supply the retina, and in the fœtus sends forwards a twig to the lens. It is accompanied everywhere by corresponding veins.

Other nerves are distributed to the eye, which are connected with the nutrient and other actions of the eyeball. These are derived from the ophthalmic division of the fifth, from the third pair, and from the sympathetic. It is remarkable, however, that all these nerves, with two exceptions, between their origin and their distribution in the globe of the eye, meet in a small ganglion situated on the outer side of the optic nerve, called the *ophthalmic* or *lenticular* ganglion. This body is usually considered a portion of the cephalic division of the sympathetic; it is connected with the superior cervical ganglion by a long branch which ascends from the carotid plexus along the carotid artery, and enters the orbit. A long nerve from the nasal branch of the ophthalmic division of the fifth also joins this ganglion at its superior and posterior angle, and a short thick branch from the third nerve joins the ganglion at its inferior posterior angle. From the anterior angles of the ganglion thus formed, proceed two bundles of delicate nerves, from twelve to sixteen in number (*ciliary nerves*), which, after having pierced the sclerotic at its posterior third, pass between that tunic and the choroid, and are distributed chiefly to the ciliary muscle and iris, but also to the cornea.

From the nasal branch of the ophthalmic there proceed two long nerves, called *long ciliary nerves*, which do not form any connexion with the ophthalmic ganglion. These nerves pass off in company, but soon separate from each other, one going to the inner, the other to the outer side of the eyeball; they penetrate the sclerotic, and accompany the other ciliary nerves in their distribution to the ciliary muscle and iris.

The eye is moved by six *muscles*, four straight and two oblique. The former arise from the margin of the optic foramen, at the apex of the orbit, and are inserted into the sclerotic near the cornea, above, below, and on each side. The superior oblique arises with the recti, but has its direction changed by a pulley of fibrous tissue at the upper and inner part of the margin of the orbit; whence it passes backwards, outwards, and downwards, under the superior rectus muscle to the sclerotic behind the transverse median plane of the globe, between the superior and external recti. The inferior oblique arises from the lower part of the margin of the orbit about its inner third, and passing backwards, outwards, and up-

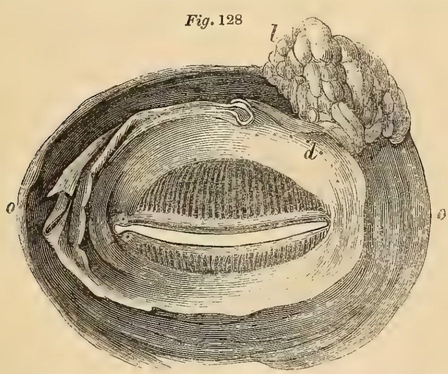
wards, under the inferior rectus, is inserted into the sclerotic, near, but beneath the superior oblique. The action of the recti muscles is obvious: when used in concert, they fix the eyeball; when singly, they turn it towards their respective sides. The globe, besides being imbedded in fat, is suspended or slung in a capsule of fibrous tissue, with which it is in immediate contact. This is attached in front to the tarsal cartilages, and is prolonged backwards over the globe and optic nerve, after being perforated by the muscles. Mr. O'Ferrall, who has lately directed attention to this fibrous structure, has termed it the *tunica vaginalis oculi.* It is important, as furnishing support to the eyeball under muscular movements. The recti muscles are supplied by the third pair of nerves, except the external, which receives the sixth. The oblique muscles antagonize the recti, and must in addition, if acting together, draw the globe inwards, and converge the axes of the eyes. The superior oblique, if alone, would most probably direct the front of the eye downwards and outwards, and the inferior oblique upwards and inwards; but on these points much difference of opinion still prevails. The former is supplied by the fourth pair, the latter by the branch of the third that gives the motor fibres to the ophthalmic or lenticular ganglion, from which the ciliary muscle and iris receive their nerves. And, in connexion with the latter arrangement, it is interesting to remark that the pupil contracts when the eyes are directed inwards and upwards, and generally also in the adjustment for near vision, which is attended with a convergence of the optic axes. During sleep the eyes are usually turned inwards and upwards, and the pupil is contracted—actions produced through the medium of the inferior division of the third pair supplying the inferior oblique and iris. The iris is evidently involuntary in its movements; it contracts only in obedience to the stimulus of light upon the retina, or when the eye is turned upwards and inwards.

The *eyelids* are exquisitely adapted to shield the eye from too strong light, and to protect its anterior surface from the contact of hurtful substances. In the upper lid, which is much larger and more moveable than the lower, there is a thin sheet of cartilage, curved to fit the front of the eye, and to facilitate its gliding motion over the globe. To the posterior convex border of this *tarsal cartilage* the levator palpebræ muscle is attached, which thus serves to elevate the whole lid. The lower lid possesses a very narrow slip of cartilage, which meets the upper at each side through the medium of fibrous tissue, which, at the outer angle of the eye is attached loosely to the malar bone, and at the inner angle forms a tendinous

cord, the *tendo oculi*, about a quarter of an inch long, which passes horizontally to be fixed to the nasal process of the superior maxillary bone. This latter is the principal attachment of the eyelids. The eyelids enclose the orbicularis muscle between the skin and their cartilages. Its fibres run in curves from the lower border of the tendo oculi and neighbouring part of the border of the orbit, encircling the eye and forming a thin layer under the skin, both of the lids, cheek, and brow, and returning to the upper border of the tendo oculi. They are supplied by the portio dura, and perhaps by some fibres of the fifth nerve, and act generally in answer to the stimulus of air or foreign particles on the fifth nerve in the conjunctiva, as well as of a too strong light upon the retina. The will exerts a limited power over the orbicularis, but is quite unable to restrain its action when sufficiently excited by the before-named stimuli. The entire muscle consists of striped fibres. The lids are further armed along their free margin by the delicate curved hairs, called the lashes. These intercept the entry of foreign particles directed against the eye, and assist in defending the organ from excess of light.

At the border of the eyelids, the skin becomes continuous with their mucous lining, termed the *conjunctiva*. This membrane lies upon the tarsal cartilages, and is then reflected over the front of the globe, where it has been already in part described with the cornea. Between the cartilages and the conjunctiva, and partially imbedded in the former, are the *Meibomian glands*, which may be seen through the conjunctiva (figure 128). Each gland consists of a series of follicles, arranged upon an elongated common duct, which empties itself on the border of the lid. They consist of a basement membrane and an epithelium (fig. 129); the latter contains sebaceous matter in its cells, and is in continual course of formation. Its particles, when fully developed, are thrust forward along the duct, and constitute the secretion. The

Fig. 128

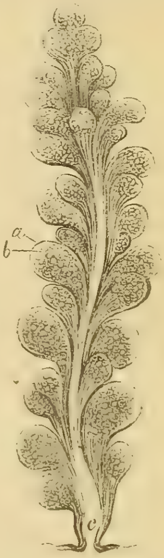


View of the conjunctival surface of the Eyelids. The Meibomian glands are seen running towards the edges of the lids:—*l*. The lacrymal gland removed with the lids. *d*. Orifices of its seven ducts on the conjunctiva. At the inner extremity of the borders of the lids the orifices of the canaliculi (puncta lacrymalia) are seen. *o*, *o*. Orbicularis muscle beyond the lids. —From Sœmmerring.

use of the Meibomian glands is obviously to prevent adhesion of the lids; and their arrangement side by side, so as to form an even layer, adapts them to the surface of the globe, over which they are being constantly moved. They are a variety of the cutaneous sebaceous glands, which they resemble in every particular, except shape. At the inner canthus is a large-sized sebaceous gland, covered with mucous membrane, and usually termed the *caruncle* (fig. 130).

The conjunctiva of the lids presents on its free surface a minute papillary structure, probably connected with the exquisite sensibility which renders this membrane so valuable a covering to the eye. In the disease termed *granular lids*, these papillæ are hypertrophied. To the sclerotic coat the conjunctiva is loosely attached by lax areolar tissue in which numerous tortuous vessels lie.

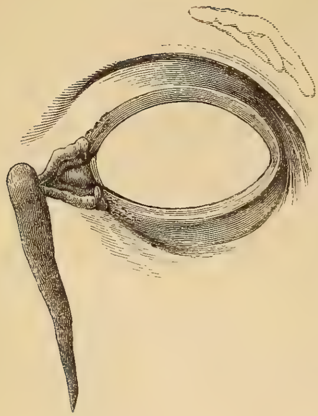
Fig. 129.



One of the Meibomian glands of a Fœtus of five and a half months: — *a.* Basement membrane of the follicles. *b.* Epithelium constituting the secretion. *c.* Orifice of the common duct. —From a specimen prepared by Dr. Goodfellow. Magn. 30 diameters.

The front of the eye is irrigated by the lacrymal fluid secreted by the gland of that name. This gland is placed within the orbit, under cover of the external angular process of the frontal bone, and is about the size represented in fig. 128, *l.* In appearance and structure it has much similarity to the salivary glands; its ultimate parts being vesicular. Its ducts, about seven in number, open on the conjunctiva, at its upper and outer part near its reflexion on to the globe, and are arranged in a row, so as to disperse their secretion over the membrane (fig. 128, *d*). The constant motion of the upper lid facilitates the distribution of the fluid, which thus streams continually over the front of the eye, and carries off any extraneous particles that may have found their way into it. The fluid is then conducted into the nostril through a singular system of channels, lined by mucous membrane, continuous between that of the eye and nose. Near the inner end of the border of each tarsus there is an orifice, a little prominent, and projecting slightly backwards, so as not to be obstructed when the lids are closed. These are the *puncta lacrymalia* (figs. 128 and 130). They lead by two ducts (*canaliculi*), into the *lacrymal sac*, a cavity formed by the lacrymal and superior maxillary bones, completed by fibrous membrane. This is continued, under the name of *nasal*

Fig. 130.



Anterior view of the Lacrymal Apparatus.—The lacrymal gland is shown in outline. At the inner canthus are the puncta and canaliculi, with the caruncula between them. The lacrymal sac forms the upper third of the vertical tube, and the nasal duct the remainder. These parts are separated within by a fold of the lining membrane.—From Sœmmerring.

duct, into the inferior meatus of the nose, where it opens under cover of the lower spongy bone. A fold of mucous membrane usually guards its orifice.

*Of the phenomena of vision.**—The consideration of the changes produced in the rays of light passing through a double convex lens explains, to a great degree, the phenomena resulting from the passage of the rays through the dioptric media of the eye.

A ray, falling on the surface of such a lens, is bent towards the perpendicular to the point of incidence, and continues in that direction to the opposite surface

* The following laws affecting the passage of rays of light through transparent media of various density ought to be kept steadily in view by the student of the physiology of vision.

1. A ray of light, in its passage from a rare into a dense medium, is bent, or, in optical language, refracted, *towards* the perpendicular to the point of incidence, if it fall obliquely upon the surface of the latter medium. The direction of the ray, therefore, is altered in the dense medium. The degree of this refraction depends partly upon the density of the medium, and partly upon the angle at which the ray falls upon it (the angle of incidence). If the ray of light fall upon the transparent surface at right angles to it, it will pass through it without undergoing any change in its direction.

2. If the ray pass from a dense to a rare medium, it will be refracted *from* the perpendicular to the point of incidence.

3. It is obvious, from what has been stated, that the incident and refracted ray will be always on different sides of the perpendicular.

4. In all cases where rays of light pass from one transparent medium to another, a certain portion of them is reflected at the surface of each new medium. If, therefore, light pass through many different media in succession, much of it will be completely diverted from its original direction by *reflexion.*

5. In general, the greater the specific gravity of a body, the greater is its refracting power.

6. If a pencil of rays diverging from a luminous point fall directly upon the surface of a convex lens, they will not all be equally refracted. The central ray will pass through unchanged in its course. Those nearest the centre will be least refracted; those most distant from it (which consequently fall with the greatest obliquity upon the surface of the refracting medium) will be most refracted.

7. On the emergence of the rays of light from a bi-convex lens into air, or any other medium less dense than the lens itself, each ray will be bent away from the

of the lens. It then emerges from the lens, and, in thus passing from a dense to a rare medium, it is bent from the perpendicular to the point of emergence. It can thus be shown that the component rays of a pencil, diverging from a point, will be bent towards the central ray of the pencil, or that which falls perpendicular to the convex surface, and be brought to a focus in the line of the central ray. And the several pencils of rays, proceeding from different points of an object, cross one another in traversing the lens, so that the foci to which they are respectively brought beyond the lens are in positions the reverse of those from which they set out, and the entire image is a reverse of the object.

perpendicular to the point of emergence. The effect of this is to cause a convergence of all the emerging rays towards the central ray; at this point of convergence, or *focus*, an image of the luminous point from which the rays originally passed is formed.

8. This point of convergence, or focus, varies as to its distance from the surface of emergence, according to the refracting power of the lens, the amount of curvature of its surfaces, and the distance of the luminous body. Its distance constitutes the focal length or distance of a lens.

9. In consequence of the unequal refraction of rays passing through a convex lens, the focus of convergence of the central rays is more distant from the surface of the lens than that of the peripheral rays. Hence the image formed at the focus of the lens is in some degree indistinct at its edges. The imperfection is due to what is technically called *spherical aberration;* and it can be counteracted only by intercepting the passage of the circumferential rays, or by employing such a combination of lenses as will establish a just proportion between the refraction of the central and peripheral rays. This aberration is liable to occur in all forms of lenses, whether convex or concave.

10. White light is compound, and may be analysed by passing a beam of sunlight through a prism. The solar *spectrum* thus formed on a surface opposite the prism is composed of bands of different colours insensibly passing into each other, which are, beginning from above, violet, indigo, blue, green, yellow, orange, and red. Of these different coloured rays, that which is most bent from the original direction of the solar beam is the violet, and the red is the least refracted. It is owing, therefore, to this unequal refrangibility of the different kinds of simple light that we are enabled to decompose white light by its transmission through a prism.

11. If the different coloured rays which have emerged from the prism be allowed to traverse a second similar prism, held in a reversed position, they will on their emergence unite to form white light again.

12. The different refrangibility of the rays of simple light is another source of indistinctness in images formed by the transmission of light through lenses with curved surfaces. The images are fringed by prismatic colours. It is called technically *chromatic aberration;* and may be corrected by means analogous to those adopted for correcting *spherical aberration.* It is obviously of great importance in all optical instruments for aiding or increasing the powers of vision that they should as much as possible be free from these sources of imperfection.

To apply this to the eye.—If a luminous object, as the flame of a candle, be placed eight or ten inches in front of the organ, some rays fall on the sclerotic and are reflected; the more central ones fall on the cornea: some are reflected, and others pass through it, are slightly converged by it, and enter the aqueous humor, which, being probably of the same refracting power, does not alter their course. Passing onwards, some meet the iris and are absorbed or reflected by it, whilst others advance through the pupil. Thus rays, falling on a large extent of the cornea, are converged so as to fall on the lens. By the convexity of the surface of the lens, as well as by the greater density of that body towards its centre, this convergence is much increased. Lastly, by their passage into the rarer medium of the vitreous humor the rays are further converged by the refraction of each ray from the perpendicular to the point of incidence, and the several pencils which they form are brought to as many foci in the retina. And still further, the rays from the opposite points of the luminous object, by reason of the change of direction which they undergo through these successive refractions, cross one another, (the angle of crossing being called *the visual angle*,) and thus the image of the flame on the retina appears inverted.

This inversion of the image may be exhibited by a model, representing the transparent media of the eye, with a retina of ground glass; or it may be shown on a recent eye by simply removing the opaque coats behind the retina, or in the eye of a white rabbit, after removing the muscles and areolar tissue around it.

When the retina corresponds, or nearly so, to the points of convergence of the several pencils of light, *distinct* vision of the object is obtained; and the distance for distinct vision is ordinarily about ten inches. If that distance be increased or diminished (no change being produced in the eye), vision is indistinct; for when the object is removed to a greater distance from the eye, it is obvious that the focus will be moved forwards, or will fall short of the retina; and when the object is approximated, the focus will be moved backwards or beyond the retina: in both which cases the same point of the retina will receive rays from several points of the object. Hence it is, that when the eye is adapted to distinct vision at a distance of ten inches, we cannot distinctly see objects at a greater or less distance. From the cause of this, which has been just alluded to, however, it is evident that, provided the rays unite very nearly on the retina, vision, especially of large objects, may prove sufficiently distinct, although not perfectly clear. Hence the distinction of Jurin between *distinct* and *perfect* vision is worthy of being borne

in mind. Distinctness of vision will depend on the size of objects, as well as on their distance from the eye; perfection of vision, on their distance alone.

This leads to the consideration of one of the most admirable provisions for the extended utility of the organ; viz. its capacity of adaptation, under the influence of the will, to distinct vision at every distance beyond that of a few inches. We have the power of producing some change in the eye by which its focal length is modified to suit the varying angle at which rays from surrounding objects fall upon it. Many different explanations have been attempted of the mode in which this adaptation is effected, of which may be mentioned that of Jurin, Ramsden, and Home, that the cornea undergoes a change in its curvature, becoming more convex for near objects: and that of Des Cartes, Albinus, Hunter, and Dr. Young, who considered the lens muscular, and to possess within itself the power of changing its curvature.

Others, again, ascribe this power of adaptation to the iris, the motions of which might, as Knox supposed, alter the curvature of the lens; or, according to Sir David Brewster, cause the lens to change its place, and come forwards during contraction of the pupil. A change in the position of the lens has also been supposed to occur from contractions in the ciliary processes or zonula, and many have contended that the entire eyeball may alter its relative dimensions by the action of its muscles.

It is conceivable that any of these changes, could they be proved actually to take place, might be sufficient to account for the effect; but, in estimating their relative value, the greatest importance is to be attached to the anatomical evidence by which they may be supported. In the eye of the bird, the ciliary muscle, from its position and attachments, must necessarily approximate the lens to the cornea; and the reasons for considering the same part muscular in mammalia, and, if so, for ascribing to it the same function as in birds, have been already mentioned, and appear to us conclusive. We, therefore, on anatomical grounds alone, adopt this view, ably advocated by Porterfield,* conceiving that when the eye is intent on near objects, the ciliary muscle is contracted, the lens advanced towards the cornea, and the latter membrane, perhaps, rendered more convex by the traction of the muscle on its border by means of the cordage of the posterior elastic lamina; while in vision of remote objects the lens is carried back towards the retina by the elasticity of the neighbouring parts. It is interesting to notice that this adjusting

* Treatise on the Eye. Vol. i. p. 446.

faculty of the eye is greatly impaired or altogether lost by extraction of the lens, or by paralyzing the ciliary and iridial muscles by belladonna. Dr. Clay Wallace considers that the ciliary muscle advances the lens by compressing the veins, and thus causing an erection or lengthening, of the ciliary processes.

It has long been observed that the pupil is very prone to contract during near vision, and to dilate when the organ is adapted to view remote objects; and it has been imagined that this change is the necessary condition of adaptation, and may affect the lens through the ciliary body. In some persons, however, not at all deficient in the adjusting power, the iris continues to oscillate for some time after the eye is adjusted, without disturbing vision; and we have occasionally found the pupil to remain dilated, though a near object is being gazed at and the illumination remains the same. Moreover, the action of light on the pupil has no effect on the adjustment of the eye, since we can continue to see an object distinctly, whether it be viewed by a strong or by a feeble light.

These facts are sufficient to prove that the movements in the iris, usually coincident with the act of adjustment, are not the cause of that act. They seem rather to be of the nature of associate movements, produced by the close connexion of the iris with the ciliary muscle, and by the community of source from which both these derive their motor nerves, viz. from the third pair, through the ophthalmic ganglion. And it is an important circumstance, that certain consensual movements of the eyeballs, performed through the medium of the third pair, are likewise associated with the act of adjustment. The movements of the iris chiefly minister to another function, the regulation of the quantity of admitted light.

The contraction of the pupil during near vision, by obstructing more of the circumferential rays, answers the important purpose of correcting the excessive aberration of sphericity which results from the greater divergence of the rays entering the eye from near objects.

Some persons have the power of adjusting the eye to distinct vision at different distances, either to a very limited extent or not at all; and we observe two states of vision connected with this defect, which are generally dependent on certain physical conditions of the lenses of the eye: these are shortsightedness, or myopia; and longsightedness, or presbyopia.

Myopia.—Thus, we meet with many persons who cannot distinctly see a yard before them,—who fail to recognize the features of their acquaintances in the street. In reading, they are obliged to bring the book close to their eyes: in looking at an object at all

distant, they exhibit a characteristic winking (μυω, connivo). Myopia occurs in adolescence, and is accompanied with a too great refracting power of the media so that the image is formed anterior to the retina. In order, therefore, to throw back the image on the retina, the object is brought very close to the eye; or the convergence of the rays of light may be diminished by the use of a concave lens.

It seems probable that the state of myopia may be acquired by the habit of looking intently at small and near objects, and that the common practice of remedying the inconvenience by the use of concave glasses tends to increase the defect. Frequent exercise of the eyes on remote objects has, no doubt, the effect of making them far-sighted. It is a common error to say that myopia disappears naturally in advanced life.

Presbyopia.—Others again imperfectly distinguish near objects, whilst they see distant ones very plainly, and the distance at which they can see distinctly is sometimes very great. Persons thus affected cannot read small print with the eyes unassisted, and they prefer holding the book at a distance. This condition of vision is connected with a too flat cornea, a deficient aqueous humor, or a flattening of the lens; and it is in a great degree accounted for by the diminution in the refracting power thence resulting, so that the focus is behind the retina. It belongs to the advanced periods of life. It may be corrected by convex glasses, which increase the convergence of the rays of light.

It is manifest that neither of these defects is dependent on the muscular apparatus of adjustment, but rather on the curves of the refracting media, which throw the organ in one direction or the other beyond the range of the adjusting power with which it is provided. When the refracting media are optically corrected, as by the use of glasses, the adjusting faculty can be exercised.

In the eye, considered as an optical instrument, there are other powers besides those already named, which serve to make it more perfect, and to place it in favourable contrast with the most successful creations of human ingenuity.

One important office of the iris is to prevent the passage of rays through the circumferential part of the lens, and thus to obviate that indistinctness of vision which would arise from *spherical aberration*, or that unequal refraction which results from the difference in the angle of incidence of the several rays on a curved surface. In this respect it resembles the diaphragms used in optical instruments. By its position, close to the surface of the principal lens,—and

behind or within the first one by which the light is converged, viz. the concavo-convex one formed by the cornea and aqueous humor,—it is adapted to admit the greatest quantity of light to the lens, consistently with the correction of the spherical aberration.

The aberration of sphericity is further obviated by the increased density of the lens from its surface towards its centre, so that the rays falling on its middle region are made more convergent as they traverse it, than those passing near its border.

Chromatic aberration, or that which occasions a coloured image by the inequality of the refraction of the elementary colours of white light by the same medium, is in some way prevented in the human eye, when adjusted to distinct vision.

The image formed by a convex lens is slightly coloured at its margin. This colouring is corrected in practice by a compound arrangement of lenses differing in shape and density, of which the second, while it continues the convergence of the rays from their original course, re-associates the dispersed colours and recomposes the white light.

The achromatism of the eye may be in part due to the diversity of shape and density of the refractive media, which seem to bear some analogy to the system forming the achromatic object-glass of Herschell. This is formed of a double convex lens of crown-glass, with surfaces of unequal curvature, the more convex being turned towards the object ; and of a concavo-convex of flint-glass, the concave side of which receives the lens of crown-glass while its convex side is towards the eye. The cornea and aqueous humor form a concavo-convex lens which differs in density from the crystalline.

It is possible that the greater density of the inner fibres of the lens may likewise share in producing the effect. But this entire subject is involved in much obscurity, and it is right to add that some very high authorities, including Sir D. Brewster, deny that the chromatic aberration receives any correction in the eye ; that, in fact, it exists in all cases, and is imperceptible only in consequence of its being so slight. It may be observed that when the eye is not adjusted to distinct vision, a coloured fringe is seen around objects. If the eye be fatigued and incapable of adjustment, or if belladonna be used, then colours are seen.

The rays of light which have now been traced to the retina, although they come to a focus in that membrane, yet can scarcely, from its extremely thin and transparent nature, be said to form *an*

image upon it. The image, however, which becomes visible in the experiment on a dead eye, though partly due to the opacity the retina acquires soon after death, is yet an evidence that this membrane does not give passage to the light, like transparent glass, or the humors, but rather like ground glass, dispersing and reflecting some portion, as indeed its peculiar texture must dispose it to do. The pink colour of the pupil in albinos shows the reflexion that occurs in those cases from the vascular choroid and retina; and Mr. Cumming has recently pointed out that in the eyes of all persons, where the pupil is tolerably large, a very decided reflexion from the bottom of the eye may be observed under favourable circumstances. To make it apparent he places the individual at a distance of ten feet from a single gas-light or lamp, and directing him to look a little on one side, a strong glare becomes visible to any one standing almost directly between him and the light. In some persons this glare is exceedingly brilliant, like that from burnished brass; in others it is fainter. This reflexion can hardly be regarded as important in a physiological point of view. It probably proceeds from the hyaloid membrane, the retina, and from the choroid also, but from the latter more or less according to the amount of pigment present in the particular instance. It is remarkable that these reflexions do not interfere with the perfection of the sense, do not derange the integrity of the impression resulting from the first passage of the rays. Corresponding but more vivid reflexions from the *tapetum lucidum* in certain animals serve an useful purpose, by giving an additional stimulus to the retina, where but a feeble light is admitted to the organ.

Excitability of the Retina, and of the allied nervous parts.—When the retina is stimulated, we have the sensation of light, whatever may be the nature of the stimulus applied. Pressure, for instance, made on the side of the eye in the dark, gives rise to the sensation of a spot of light, the situation and size of which will be determined by those of the point of the retina touched. The same is true of the optic nerve, and of certain parts of the encephalon with which the nerve is connected. The sensation of light, then, consists in a recognition by the mind of a certain condition or affection of these nervous parts, and this condition may be induced by the application of any of the ordinary stimuli of nerves. The retina, however, is capable of being affected in this way by the luminous rays; and perhaps this capacity is dependent on the peculiar manner in which the nervous matter is spread out in this part. However that may be, the light incident on the retina is the only stimulus which

can naturally affect it ; and the other parts, endowed with the same kind of excitability, can, in the natural state, be stimulated only in a secondary manner, as though by induction through the retina. It is certain that the integrity of these other parts is essential to vision, and it may therefore be concluded that during vision they are all, immediately or mediately, in a state of excitation.

The retina is not affected sufficiently for the purposes of vision by a very faint light ; and on the other hand, a very strong light, especially if long applied, will produce effects analogous to those resulting from an inordinate stimulus to other organs: the blood-vessels of the retina will become unduly injected, its nutrition disordered, and even its texture destroyed. But the retina exhibits a considerable power of accommodation to different amounts of light, and thereby the utility of the organ is much enhanced, as well as its safety provided for. After a short stay in the dark, objects disclose themselves, which at first were imperceptible; and, on the other hand, a light which was at first too bright, becomes agreeable by use. This adaptability is quite independent of the iris, and has its analogue in the case of every nerve of sense.

The *iris*, however, by its contractile power, is a most important agent in protecting the retina from the effects of sudden transitions from dark to light ; and in thus co-operating for the maintenance of its most essential quality, excitability, the iris is seconded by the eyelids and brows. The iris contracts under a strong light, by virtue of the stimulus imparted to the retina ; for if this or the optic nerve be destroyed or paralysed, as in amaurosis, the iris no longer contracts. It is interesting, however, to notice that the iris of the unsound eye will often contract in company with its fellow, when the opposite sound retina is stimulated. The motion is therefore evidently caused by a reflexion of the stimulus from the optic nerve, through the nervous centre along the inferior branch of the third pair to the iris, and the consensual action of the two sides is effected in the nervous centre. Mechanical irritation of the ciliary nerves, or third pair, occasions contraction of the pupil on the same side. The orbicularis palpebrarum and corrugator supercilii likewise contract under a powerful glare, in obedience to a stimulus reflected through the optic nerve, and quite independently of the will. This is well exemplified in children affected with strumous ophthalmia, in whom the excitability of the retina is highly exalted.

The *pigmentum nigrum* is a permanent shield to the retina, absorbing the light which falls upon it, and remaining the same

under all degrees of illumination. The excitability of the retina in creatures usually exposed to the full light of day, requires this additional protection; and where it is deficient, as in albinos, an ordinary light becomes painful, and the moveable protecting parts are habitually brought into increased use. In animals of nocturnal habits, furnished with a tapetum lucidum, the excitability of the retina is probably somewhat modified, and the iris also is generally larger, and capable of an ampler range of motion.

Duration of impressions on the Retina.—We continue to see an object after the rays of light emerging from it have ceased to fall upon the retina, and this for a period proportioned to the intensity and duration of the impression they have left. The familiar experiment of twirling a lighted stick, so as to see a luminous circle, shows that the impression made by it, when at any one point of space, remains on the retina until it reaches that point again. By ascertaining the speed necessary for completing a luminous circle of a certain size we can estimate the duration of the impression; and by augmenting or diminishing the brilliancy of the ignited point its duration is found to be affected. A momentary impression of moderate intensity continues for a fraction (according to D'Arcy, about an eighth part) of a second. But if the impression be made for a considerable time on any one point of the retina, it endures for a longer period after the object is removed. It is owing to this retentive power of the retina, that the rapid and involuntary act of winking does not interfere with continuous vision of surrounding objects.

Appearances of objects remaining after the removal of the objects themselves from the field of vision, come under the head of *ocular spectra.* In figure they correspond to the image the object has thrown on the retina, but they are of the complementary colour to that of the object. Thus, the spectrum left by a red spot is green; by a violet spot, yellow; by a blue spot, orange; and these colours of the spectra are particularly obvious when the eye is directed towards a white ground. It is further remarkable, that after long gazing on a very bright light, as the sun's disc, the remaining spectrum, if viewed on a white surface, assumes the different colours in succession, from black, through blue, green, and yellow, to white: if viewed on a black surface, the order of the succession is reversed. These several phenomena can only be referred to particular states or modes of excitation of the retina, by means of which alone it is that the differences of the component colours of white light are made evident to our perceptive powers.

It appears by a simple experiment, for the principle of which we are indebted to Mariotte, that the small portion of the retina corresponding to the entrance of the optic nerve, is incapable of exciting visual sensation though it receive the image of an object. Place the thumbs together at arm's length, shut the left eye and fix the right eye steadily on the left thumb ; then the right thumb, if moved gradually outwards (so that its image on the retina of course traverses inwards), ceases to be visible in a particular spot, but is again seen beyond it. It will be remembered that the fibrous lamina of the gray nervous layer of the retina is here evolving itself from the nerve, and *is not yet invested with the vesicular or other laminæ;* a circumstance of great interest in regard to the *modus operandi* of the constituents of the retina in vision.

It has indeed been denied by an eminent physiologist, that the retina is insensible to light at this point, on the ground that, if such were the case, we should see a dark spot in our field of view whenever we use only one eye. To produce the physical sensation of darkness, however, the retina seems as necessary as the nerves of ordinary feeling are to the production of the physical sensation of cold. Both sensations are occasioned by the absence of the respective stimulus, but the specially endowed nerve is as essential to acquaint us with the absence as with the presence of the stimulus. What Mariotte's experiment proves is simply that over that spot no nervous matter, having the peculiar power of excitability by light, exists ; and as far as the faculty of seeing with that spot is concerned, it is as though the piece of retina had been punched out. We no more see a dark spot corresponding to it, when we look with one eye, than we see everything dark behind us,—where there is no nervous expansion visually endowed. For, in strict language, a distinction must be drawn between the sensation of darkness and the absence of the sensation of light.

This incapacity of vision at the entrance of the optic nerve, seems to be essential to the mode of junction of the retina with the nerve, since it appears to have been the chief reason why the nerve was not made to enter in the axis of the eye. If the blind spot had been situated in the axis, a blank space would have always existed in the centre of the field of vision, since the axes of the eyes, in vision, are made to correspond. But, as it is, the blind spots do not correspond when the eyes are directed to the same object ; and hence the blank, which one eye would present, is filled up by the opposite one.

Though no other part of the retina is insusceptible of luminous

impressions, yet there is good reason to suppose that the hinder part of it is much more capable of appreciating them than the anterior. When using one eye only, we naturally direct it towards the object we wish to inspect, and in that way throw the image to the bottom of the globe. When the eye is thus fixed, objects near the boundary of the field of vision are less distinctly seen than those at its centre. The posterior part of the retina, too, is the best adapted to receive correct images through the dioptric media, and we find its gray nervous layer becoming thinner and thinner towards its anterior border.

It is probable that the most anterior part of the retina is never used in vision, since it can scarcely receive rays directly from the lens. Dr. Young, by fixing the eye in the most natural direction, viz. forwards and a little downwards, and by then moving before it a luminous object, in various directions until it passed beyond the range of vision, ascertained the range upwards to be 50°; downwards, 70°; inwards, 60°; and outwards, 90°: the extent in each direction being limited by the contiguous parts of the face. An object, therefore, occupying only an angle of 120°, both in the vertical and horizontal direction, and suitably placed, would about fill the field of vision of a single eye, when the organ was fixed as above described. Now, it may be proved that no part of the image of such an object would fall on the anterior part of the retina.

Perhaps it is only in, or very near, the axis of vision, that sight can be said to be *perfect*. The existence of the yellow spot of Sœmmerring at that point continues a riddle which the most attentive examination of its anatomy has not yet solved. And from the absence of this spot in almost all the lower animals, we are led to doubt its importance to perfect vision.

To the perfect exercise of vision, as of all the other senses, an effort of *attention* is necessary ; and this effort is naturally accompanied with a motion of the eyeball towards the object, so that the image may be thrown upon the central part of the retina. The range of motion of the eyeball Dr. Young calculated at 55° in every direction ; so that the head being fixed, a single eye may have perfect vision of any point within a range of 110°. This field is further widened by the use of the opposite organ, but beyond this an increased range is only to be acquired by movements of the entire head.

The internal, or gray nervous layer of the retina seems to be the essential part on which the power of the retina in the process of vision depends. That layer is an *unbroken sheet*, continuous by its

fibrous internal surface with the axes of the tubules of the optic nerve, and having its external surface formed by a structure similar to that of the cineritious substance of the cerebral hemispheres. Its permeation by a close network of capillaries assimilates it still further to the gray nervous matter; for which reasons it may be considered as a portion of the cerebrum advanced towards the surface of the body into a suitable relation to a dioptric apparatus for the reception of rays of light from external objects. The optic nerve may be regarded as a commissure between the gray nervous sheet within the sclerotic, and the gray nervous matter of certain parts of the cerebrum. We have no more reason to deny the immediate connexion of the sensorium with the retina, than its immediate connexion with any small portion of the cerebral convolutions, duly united with the rest. The nature of the connexions between the retina and the brain, and the phenomena to which their disruption gives rise, have been the occasion of many interesting speculations regarding the mode in which the mind is reached, or, in other words, as to how an impression on the retina becomes a sensation to the mind. But we shall probably be disappointed if we imagine that any facts which have been or may be hereafter ascertained, are capable of leading to the solution of a problem too inscrutable for our limited powers.

It is a matter of considerable interest, as regards the mode of action of the retina in vision, to determine how distant the images of two points on the retina must be, to be seen distinctly as two; in other words, how small a portion of the retina is capable of independent sensation. As the result of many experiments and calculations by Smith, Harris, and others, this may be stated as probably about $\frac{1}{8000}$ of an inch, so that the objects must subtend an angle of at least $40''$. Two points within an angle of that size would appear as one. It is a question somewhat different, what is the smallest portion of the retina capable of sensation; and undoubtedly an object whose sides subtend an angle very much smaller than the preceding may be visible, if sufficiently bright. But this circumstance of quantity of light introduces a difficulty into the inquiry, since even in a mathematical point, if sufficiently brilliant and out of focus, might become visible by its circle of aberration on the retina; although, if its rays met in the retina, it would be invisible. But, in carrying our speculations thus far, we must cease to regard the retina as a mathematical plane, and remember that it has a certain thickness, in traversing which the rays would necessarily cover more than a point, either in front of or

behind the exact focus. It is obvious that a linear object would be more perceptible than a point, and a moving object more so than a stationary one, in consequence of wider and more distant portions of the retina being affected in both cases.

The apparent truthfulness of a view, recently put forward on high authority in Germany, and copied into several works in this country, makes it necessary to explain here that the rod-like particle of Jacob's membrane, though corresponding nearly in size with the points of the retina capable of independent sensation, yet being on the choroidal surface, and separated from the gray nervous layer by the intervening granules, can scarcely have a share in determining the size of the independent visual points. The unfortunate error which placed these rods as papillæ on the hyaloid surface of the retina, was too tempting a ground of theory not to be readily admitted as true, without scrupulous examination; and the price to be paid will probably be some degree of discredit thrown on minute anatomical research.

Correct Vision with an inverted Image.—Visual idea of Direction.—The image on the retina being the reverse of the picture of external objects seen by the mind, it is manifest that in some way or other the inversion is counteracted ere the impression becomes a sensation. It is conceivable that this correction may take place in the optic nerve or brain, but it is far more probable that it occurs in the retina. It is certain that we do not see the image as it exists on the retina, or its inversion would not have remained so long unknown; we rather see *out of* or *from* the retina. The simple experiment of pressing with the finger on the retina through the ocular tunics, and thus eliciting a luminous appearance on the opposite side, seems to prove that the apparent projection of a luminosity in a direction perpendicular to the point stimulated, is a necessary part of the excitability of the retina. If this be granted as an ultimate fact, it will explain why an inverted image, formed on a concave retina, shows objects in the same position as they are shown by the other senses which receive direct impressions from them, particularly touch.

It has been supposed by Müller and Volkmann, that objects do really appear inverted; but they argue that, as long as all do so, even visible parts of our own bodies, there is no need of a correction. But this will not explain the perfect harmony existing between impressions conveyed through the senses of hearing and touch, with those derived from sight. Sounds are appreciated, and tactile impressions are felt, as proceeding from a particular direc-

tion as regards the body—our several organs are conceived as existing in a particular relative position, altogether independently of vision—and vision accords entirely, and at once, with these senses in the determination of locality, without the necessity of an education of the sense, such as a reversed impression on the mind through the eye would require.

Were the eye and the whole body fixed, we should still have a knowledge of the relative position of visible objects, and of course of the direction in which each point of their surface was placed, as regards the organ of sense; and as rays coming from objects in the same direction as regards the body, would then always fall on the same part of the retina, we might conclude that each part of that membrane had the power of conveying the notion of position in one direction only as regards the body. But the eye being a very moveable organ, we are enabled to make the image of a stationary object travel successively over a large tract of the retina without the object appearing to move; since we are conscious, through the muscular sense, of the motion in our own eye. The visual idea of direction in regard to the body, therefore, does not depend on the image falling on a particular point of the retina, but in a great measure on the muscular sense, in conjunction with that quality of the excitability of the retina already spoken of.

It is proper also to mention that the limits of the field of vision, formed by certain parts of the face, are a standard to which the mind refers in estimating the position of visible objects. The outline of the field remains the same, through all movements of the eye. The motions of the head or body can alone bring new objects into the field; and the muscular sense thus still further contributes to enhance the usefulness of the sense of vision.

Visual perception of Shape and Size.—If an object form a large image on the retina, and of a square figure, we conceive it at once to be large and square; and of this no other explanation can be given than that the visual points making up the surface of the retina have, as regards space, a relation to one another, of which the mind is intuitively cognizant in framing its ideas from visual impressions. But the size of an image, relatively to the whole retina, will vary with the distance of the object; and the conception of its real dimensions would be erroneous, were it not that the impression were corrected by the muscular sense engaged in the adjustment of the eye to distance, and by the lessons of experience. When a person, blind by cataract from infancy, is couched, he concludes that the diversified details of the scene presented to him are at an

uniform distance, as in a picture; and a species of education can alone undeceive him. He learns, through touch, that all objects are not equally near to him, and gradually familiarizes himself with the changes in their apparent size, distinctness, and colours, produced by the movements of his whole body with regard to them. The adjusting faculty is an additional source of correct knowledge.

Visual Perception of Motion in Objects. — When an object moves in a direct line, to or from the eye, its motion is inferred chiefly by the change effected in the size of its image on the retina, as when a locomotive engine, at full speed, approaches the observer. When the object moves in an arc, of which the eye is the centre, its motion is known, if the eye be fixed, simply by the movement of its image across the retina. But most motions occurring around us are known in both these ways. When, too, the attention is excited to the moving object, the eye is naturally moved in concert with it, in order to keep its image near the axis of the organ where vision is most perfect. Our appreciation of the direction and velocity of the motion is thus heightened by the exercise of the muscular sense.

Doubleness of the Organ of Vision.—The preceding account has been almost confined to the phenomena of vision with a single eye; it remains to be explained how the doubleness of the organ affects the sense.

In some animals the eyes are so placed as to look in different directions, and in these the images formed are, doubtless, independently recognized by the animal, just as are those thrown on different parts of the retina of a single eye in ourselves. But where the eyes are both directed the same way, it is manifest that a double image of each object must be received, and that the singleness of the resulting sensation must depend either on our noticing only one of these images, or else on our forming a single conception from both conjointly. It is easy to prove that the latter is generally the case, although we sometimes derive our information from the affection of only one eye.

The eyes are moved in concert by the muscles attached to them, so that their axes always converge towards the object to which they are adjusted. The consequence of this is, that the corresponding points of the two images are made to occupy corresponding points of the two retinæ, or very nearly so, and single vision is produced. If the two images are unsymmetrically placed on the retinæ, as where the optic axes do not converge to the object, a

double sensation is excited. Thus, in squinting, two impressions are excited, unless, by long habit, one eye ceases to be adjusted and employed, and gradually loses its excitability: but when two similar objects are presented to the eyes of a squinting person, one carefully in the axis of each, their images coincide and they are seen as one. The double vision of drunkenness, and of certain cerebral affections, is explicable partly on the same ground, but in such cases considerable allowance must be made for the disordered state of the sensorium. Again, if corresponding points of the two retinæ are pressed by the finger, a single luminosity is perceived; but a double one, if the points touched are non-symmetrical. Something similar to this blending of two impressions in one sensation exists in the sense of hearing, and, perhaps, also in taste and smell.

The corresponding points of the two retinæ are such as would be in contact, if the two retinæ were adapted to one another: the upper and lower parts correspond with the upper and lower, and the inner side of one with the outer side of the other.

As we are entirely ignorant of the mode in which the mind takes cognizance of a single impression on an organ of sense, we cannot hope to understand how a single sensation can result from a double impression. But it is most interesting to remark a structural peculiarity in the course of the optic nerves, which certainly allies itself with this wonderful part of their function. Their partial decussation in the chiasma, or commissure, connects each retina with both optic tracts, and with the corresponding portions of the cerebrum; and it is not improbable, as Dr. Wollaston conceived, and Mr. Mayo has described, that the right side of both retinæ is continuous with the right optic tract, and the left side of both with the left. This would place each side of the central apparatus in connexion with its own side of both the symmetrical images, and might be supposed to favour their conception as one. Dr. Wollaston relates, that on different occasions he lost the power of seeing one half of an object to which he directed both eyes; and others have experienced similar temporary attacks. Thus, Abernethy would humorously affirm that he could sometimes see only his *ne* and *thy*, having lost the other members of his name. Such phenomena are readily explained by supposing the anatomical arrangement of the sides of the retinæ, with regard to the optic tracts, to be such as above described, since any derangement of one optic tract would then affect the same part of both optic images. Indeed, in Dr. Wollaston's own case, a tumor was found involving one of the optic

tracts, as he had himself inferred from the phenomenon above mentioned.

What we have before advanced, however, regarding the unbroken sheet of gray nervous matter in the retina, leads us to attach even more importance to the commissural fibres which appear to connect the two retinæ together, through the medium of the chiasma, and independently of parts behind it. We conceive that these commissural fibres may connect corresponding parts of the retina, much in the same way as corresponding parts of the cerebral convolutions of the opposite hemispheres are linked together by the corpus callosum or other commissures; and that the unity of action of the double organ may depend, as to its physical cause, on the same principle in both.

This capacity of forming a single conception from a double impression may appear, at first sight, to be given simply to obviate confusion; but Mr. Wheatstone has most ingeniously shown that it confers a new power on the sense, viz., that of appreciating forms projected in relief.

Such objects, if sufficiently near the eyes for the optic axes to converge in viewing them, are seen from two different directions: they are represented on each retina by a different perspective projection; and the more so, the nearer the object to the observer.

Mr. Wheatstone has shown that the single sensation excited by these two images is that of a third image different from them both, but excitable only by both of them at once, and attended with the notion of solidity, or projection in relief. He has illustrated this by an instrument which he terms the *stereoscope*. Some object of three dimensions (as a cube) is represented in two drawings as it would be seen at a small distance by each of the two eyes. These drawings are then placed symmetrically in the right and left compartments of a small box, so as to be reflected by sloping mirrors to the eyes of the observer, each view to its corresponding eye. When he looks at each separately, it seems a mere drawing on a flat surface; but when he regards both views at once, they appear to coalesce, and a solid prominent figure seems to occupy their place. Mr. Wheatstone has also shown that the same effect occurs, although there may exist some disparity between the size of the two images; and that the resultant idea is that of a figure of intermediate size. Now, unless an object is placed directly in front of the eyes, its image is larger in one eye than the other, because it is nearer one eye than the other; and this faculty of

striking a mean between the two impressions is, therefore, constantly made use of.

The above facts abundantly prove the non-existence of *absolutely corresponding* points on the two retinæ, such as were formerly held to exist. But they do not invalidate what has before been advanced respecting the general correspondence of certain tracts of the two retinæ, and the absolute non-correspondence of others.

Mr. Wheatstone further observes, that if two dissimilar images are represented at once to the corresponding parts of the two retinæ, they are not blended, but seen alternately, according to their distinctness and degree of illumination. This is a very singular circumstance, and agrees closely with what takes place when dissimilar colours are viewed in the same way.*

* On the subjects treated of in this chapter reference is made to the following works: Zinn, Descriptio Anatomica Oculi Humani; Haller, Elementa Physiologiæ, tom. v.; Porterfield on the Eye and Vision (an admirable work); Dr. Jacob's paper in the Phil. Trans. 1819, and in the 12th vol. Med. Chir. Trans. and the article "Eye" in the Cyclop. Anat. and Phys. by the same author; Mr. Dalrymple's Anatomy of the Eye, London, 1834; the introduction to Mr. Lawrence's Treatise on Diseases of the Eye. 2d edit. 1841; Mr. Wharton Jones' Essay prefixed to Mackenzie on Diseases of the Eye; Arnold über das Auge des Menschen; Sœmmerring's Plates of the Eye; Müller's and Wagner's Physiology; Mackenzie on Vision; Bowman (W.) Illustrations of the Anatomy of the Eye in health and disease, now in course of publication.

CHAPTER XVIII.

OF HEARING.—THE ORGAN OF HEARING.—ITS DEVELOPEMENT IN THE ANIMAL SERIES.—THE EXTERNAL EAR.—THE TYMPANUM.—THE LABYRINTH.—THE FUNCTIONS OF THESE PARTS.

It is by the sense of hearing that the mind takes cognizance of those oscillations of elastic matter which give rise to the phenomena of sound.

The communication of these oscillations to the ear may take place through the air, or through the intervention of some solid conductor, brought into immediate connexion with the organ of hearing.

The essential part of the organ of hearing is a sac, containing fluid, upon which the nerve of hearing is freely distributed: this sac being in connexion with the cranial parietes. This is represented in the human subject by that small cavity which is excavated in the petrous portion of the temporal bone, called the *vestibule.* This, and *three semi-circular canals*, with a spirally disposed canal, divided by a partition, constituting the *cochlea*, form the *labyrinth.* External to this, and situate between the squamous and petrous portion of the temporal bones is a cavity, *the tympanum,* which in front further communicates very freely with the cavity of the throat through an open channel, *the Eustachian tube*, whereby air has a free access into the tympanum. This cavity is closed on the outside by a membrane (*membrana tympani*) which extends over its external orifice as over a drum. A communication is established between the membrane and the inner wall of the tympanum, by a chain of small bones which extends from the one to the other. These are the *ossicles* of the ear. The outer bone of the chain is intimately attached to the membrana tympani, and the inner one to a membrane which closes the vestibule on the outside. The three bones which compose the chain are articulated by moveable joints, and are moved by small muscles, which are thus enabled to regulate the tension of the membrana tympani, as well as of the membrane of the vestibule. Externally is an apparatus for collecting sounds and conducting them to the tympanum.

Developement of the Organ of Hearing in the Animal Series.—There is no organ in the body in which we find a more remarkable gradation of develope-

ment in the various classes of animals, than in the ear. We see it existing as a simple sac in the cephalopod and gasteropod mollusks, and in crustacea. In the cuttle-fish, it consists of a small sac filled with fluid, lodged in a chamber excavated in the cranial cartilage. The chamber is closed everywhere except at the entrance of the auditory nerve, which passes in to expand upon the sac. From its inner surface there project several obtuse processes, of a soft, elastic nature, which support the sac. The sac contains a calcareous body or *otolithe.* Even at this early stage of developement the organ is double, and the two cavities are separated from each other by a very thin septum. It is obvious that these cavities are strictly analogous to the vestibule in the higher classes.

In Gasteropoda, the organ consists of a sac, to which the nerve is distributed, and which contains fluid and several small otolithes, which, according to Siebold, exhibit remarkable movements.

In Crustacea, the organ still exists as a simple sac. This, as Dr. Arthur Farre has shown, is situated, in the lobster, in the base or first joint of the lesser antenna. Its place is indicated by a tough membrane which covers an oval aperture in the upper surface of this joint; the membrane being a continuation of the same structure which forms the shell, but in which the earthy matter is wanting. Towards the inner and anterior margin of this membrane, there is a small round aperture, through which a bristle may be passed. "On removing this oval membrane, together with a portion of the surrounding shell, the internal organ is brought into view, completely imbedded in the soft integument and muscular structure of the antenna." It consists of a sac, in shape like an auricle, and of a horny structure, like soft quill, suspended in the centre of the joint, free on all sides, and having only a single attachment near the aperture in the oval membrane already described; it nearly fills the cavity of the joint. The sac contains particles of siliceous sand, which find their way into it through the aperture already described, and probably fulfil the office of the otolithes which exist in other classes of animals. Numerous very remarkable ciliated processes are attached to the lower surface of the vestibular sac: they are arranged in a semicircular line. In the neighbourhood of this line the auditory nerve attaches itself to the sac, and forms a plexus, which covers the whole under surface of the sac, extending also towards its upper surface. The nerve is derived from the lesser and greater antennal nerves.

Dr. A. Farre has shown that the cavity situate at the base of the greater antenna is not, as has been hitherto supposed, suited to act as an organ of hearing. It is a conical papilla, abruptly truncated, and having stretched over it a membrane, which is pierced in its centre by an aperture capable of admitting a small bristle. On making a section of this part, nothing more is seen than a narrow canal in the fleshy substance leading perpendicularly from the external orifices, and terminating abruptly at the depth of two lines. A nerve is sent off to this organ from the supra-œsophageal ganglion. Such an organ is very ill-adapted for hearing. Dr. Farre has ascertained that this is the most sensitive part of the body of the lobster; "since, while the mechanical irritation of any other parts excited only a slight movement in the limbs of the animal, when out of water, and somewhat feeble, the touching of this part was immediately followed by a violent and almost spasmodic flapping of the tail."*

* Farre on the Organ of Hearing in Crustacea. Phil. Tr. for 1843, p. 233.

In Fishes the organ of hearing acquires a considerable increase in the complexity of its organization. It consists of a vestibular sac, with the accession of, in general, three semicircular canals. In the myxine, however, a fish of very low organization, there is only one of these canals. In the lamprey there are only two. The vestibular sac consists of a large sac (*utriculus* of Breschet), into which the semicircular canals open, and with the walls of which they are continuous, and of a small offset from this larger one (the *sacculus* of Breschet). This apparatus is composed of a thin, transparent, elastic membrane. It is filled with fluid, and contains in each sac, either porcelainous bodies (*otolithes*), of beautiful structure and great diversity, as in the osseous fishes, or masses of pulverulent deposit, like powdered chalk (*otokonia*), as in the cartilaginous fishes. These, whether hard or soft, consist of carbonate of lime, and therefore may be quickly decomposed by a mineral acid. The whole of this auditory apparatus is deposited in an excavation of the cranial wall, which communicates with the cavity of the cranium itself, excepting in the rays and sharks, in which it is enclosed by the cranial cartilages. It is suspended in fluid (part, probably, of the cerebro-spinal fluid), which constitutes the analogue of the perilymph in the higher animals. In some fishes, according to Breschet, an additional offset from the larger sac exists, to which he gives the name *cysticule*. All these parts are analogous to the membranous labyrinth of the higher animals, there being nothing to represent the tympanum or the cochlea. In many of the osseous fishes the auditory apparatus has no communication whatever with the exterior. In rays and sharks, however, a prolongation of the labyrinth extends through an opening in the occipital portion of the skull to the surface just beneath the skin. In many fishes, according to Weber, there is an intimate connection between the auditory apparatus and the swimming bladder, although their cavities have no communication with each other.

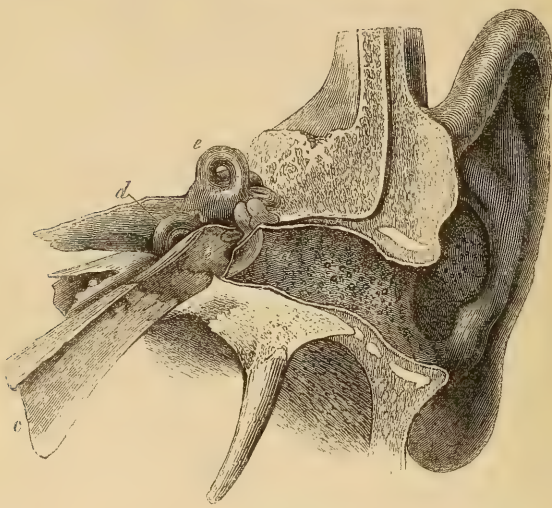
In Amphibia, the auditory apparatus is closed off from the cranial cavity, and is contained in the cranial bones. It consists of a vestibule with three semicircular canals. In some, there is placed external to this labyrinth a tympanic cavity, closed on the exterior by a membrane, which is intimately united with, or a portion of, the integument, or a thin layer of cartilage. An osseous pillar (the columella) or a chain of two or three ossicles, extends from the wall of the vestibule to this tympanic membrane, analogous to the tympanic bones in the human subject. In the Reptiles, there is a short canal connected with the vestibule, analogous to the cochlea. The existence of this canal establishes that of a second external opening belonging to the labyrinth, or *fenestra cochleæ*, in addition to the *fenestra vestibuli.* Some of the Reptiles, as the serpents, are devoid of a distinct tympanic cavity, but the existence of a columella beneath the skin indicates a rudimentary state of it. In others, as the tortoises, crocodiles, and lizards, such a cavity exists, with its usual canal of communication with the fauces, the Eustachian tube, and with a columella. The fluid of the labyrinth contains crystalline particles in place of otolithes.

In Birds, the organ of hearing has the same parts as in the higher reptiles. Its labyrinth has the cochlea and semicircular canals, and the two fenestræ, and there is a tympanic cavity with a columella. The cochlea is a very slightly bent canal, divided by a membranous septum into two passages, scala vestibuli and scala tympani.

In Mammalia, the general characters and structure of the organ of hearing closely resemble those of man.

In examining the anatomy of the human ear, we shall first describe the external ear, next the middle ear, or tympanum, and lastly, the labyrinth.

Fig. 131.



General view of the external, middle, and internal ear, as seen in a prepared section through *a*, the auditory canal. *b*. The tympanum or middle ear. *c*. Eustachian tube, leading to the pharynx. *d*. Cochlea; and *e*. Semicircular canals and vestibule, seen on their exterior, as brought into view by dissecting away the surrounding petrous bone. The styloid process projects below; and the inner surface of the carotid canal is seen above the Eustachian tube. From Scarpa.

The *External Ear* comprises the free, expanded part, *auricle*, or *pinna*, and the *auditory canal* or *external meatus*.

The *auricle* presents an outer surface, which is on the whole concave, and slightly inclined forwards. On this surface are several eminences and depressions, resulting from the folded, or rather crumpled, form of its cartilaginous basis, and which are seen reversed on the free portion of the opposite surface. These are;—a prominent rim or *helix*, and within it another curved prominence, the *anthelix*, which bifurcates above, so as to enclose a space, the *scaphoid fossa*, and describes a circuit round a deep, capacious, central cup, the *concha*. At the end of the helix, in front of the concha, is a small detached eminence, the *tragus*, so named from its bearing a tuft of hair resembling a goat's beard. Opposite this, behind and below the concha, is the *antitragus*. Below is the pendulous *lobe*, composed of dense areolar and adipose tissues. The *concha* is imperfectly divided into an upper and a lower part by the

anterior curved extremity of the helix. The *groove of the helix* is continued into the upper division, and the auditory canal leads from the front and deepest part of the lower division, where it is overhung by the tragus and its protective tuft of hairs. The cartilage of the pinna consists of one principal piece, from which that of the tragus and antitragus is separated by a fissure filled up by fibrous membrane. It is very flexible, and elastic, has a yellowish colour, and belongs to the same category as the cartilages of the alæ nasi, &c. Ligamentous fibres bind the concha behind and above, and the tragus in front to the bone and fascia in the neighbourhood. A few muscular fibres passing between different parts of the auricle, serve to impress upon them movements, but so slight as to be hardly worthy of note. These fibres are found externally on the tragus, the antitragus, the upper end of the helix, and behind on the concha. The whole of the cartilaginous part of the ear is rendered moveable by three muscles, the *superior* and *anterior auris*, arising from the epicranial aponeurosis, and converging to the concha and helix, and the *posterior auris*, passing between the mastoid process and concha.

The *auditory canal* passes from the concha inwards for about an inch, or rather more. It inclines a little forwards, and is slightly bowed, so as to be higher near the middle than at either end. Its width does not equal its height, and it is altogether narrower in the middle. The membrana tympani, which terminates it, is placed obliquely in consequence of the lower side of the meatus being longer than the upper. The canal consists of two parts, a cartilaginous and fibrous one, and an osseous. To form the first, the cartilage of the concha and tragus is prolonged inwards as far as the auditory process of the temporal bone, and constitutes a tube imperfect at the upper and back part, where its deficiency is supplied by fibrous membrane. This cartilage is rendered still further moveable by partial slits in a vertical direction (*incisuræ Santorini*). Muscular fibres are described by some to exist in the meatus, which according to Haller, becomes shortened by their contraction. The osseous part of the auditory canal consists in the fœtus of a ring of bone, to which the membrana tympani is attached (*tympanic ring* of the temporal bone). In the adult, it is nearly three-quarters of an inch long, and gives the meatus the form and direction already described.

The skin of the external ear is delicate, and well supplied with vessels and nerves. The orifice of the meatus, besides being concealed behind the tragus is defended by hairs, and a close arrangement of ceruminous glands, which furnish an abundant secretion,

calculated to entangle particles of dust, or small insects, and to prevent their entrance into the organ. These glands are principally seated in the subcutaneous tissue, where the cartilage is deficient, and do not extend into the osseous portion of the canal. The *cerumen* is an oily, very bitter substance, of a yellow colour, and contains, in addition to fat, albumen, and colouring matter, a bitter principle analogous to that of the bile. If not removed from time to time, it is liable to form hard pellets, which either impact the passage, or come into contact with the membrana tympani, and in either case seriously interfere with the transmission of sound to the internal parts. These concretions are partially soluble in ether and turpentine.

The *Middle Ear*, or *tympanic cavity*, is a space filled with air, communicating with the pharynx by the Eustachian tube, and interposed between the external meatus and the labyrinth. It opens behind into the mastoid cells, which are also filled with air, and it is traversed by a chain of moveable bones, connecting the membrana tympani with the vestibule or common central cavity of the labyrinth. The tympanum is of irregular shape, compressed laterally and lined by a very delicate ciliated epithelium, prolonged from the pharynx.

The external wall of the tympanum is formed by the *membrana tympani*, and a small extent of the surrounding bone. The membrane is nearly oval, but wider above than below, and, as already stated, placed in a slanting direction, so as to form an obtuse angle with the upper wall, and an acute one of about 45° with the floor of the auditory canal. It consists of three laminæ, an external, middle, and internal. The external is derived from the cuticular lining of the canal, and easily detaches itself with that structure after maceration. The middle is strong and fibrous, perhaps analogous to the dermal part of the integument, and attached through the medium of a dense fibrous rim to the bone, which presents a distinct groove for its reception, except above. The handle of the malleus is firmly united to this layer of the membrane, in a vertical direction as far down as the centre, and draws the membrane inwards along that line, so that its outer surface is concave, its inner convex. The abundant small vessels supplying this part run along the handle of the malleus, and thence radiate more or less directly towards the border. The fibrous tissue is in part similarly disposed, and thus seems to have led Sir E. Home to describe a radiating muscle in the membrane, which does no tappear to exist. Seen from within, a concentric arrangement of the fibres is more obvious.

The inner layer is the ciliated epithelial lining of the cavity, which is easily scraped off for examination in the fresh state (see vol. i. p. 62).

Fig. 132.

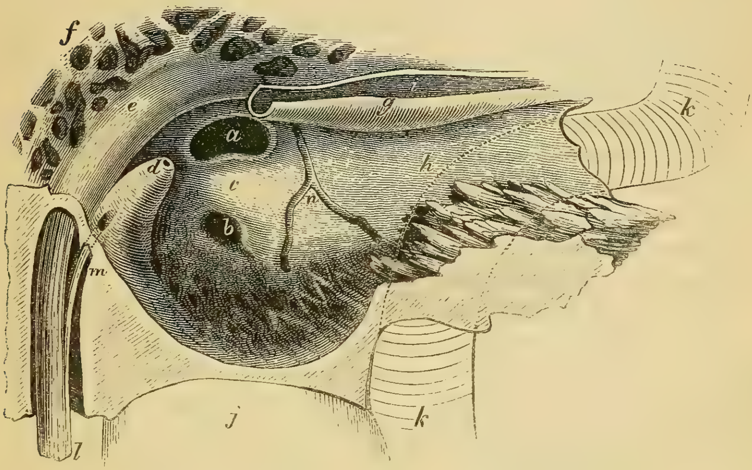


Diagram of the inner wall of the tympanum after maceration, the outer wall and ossicles being removed. *a.* Fenestra ovalis. *b.* Fenestra rotunda. *c.* Promontory. *d.* Pyramid, with the orifice at its apex. *e.* Projection of the aqueductus Fallopii. *f.* Some of the mastoid cells communicating with the tympanum. *g.* Processus cochleariformis, bounding *i*, the canal for the tensor tympani muscle: the anterior pyramid is broken off, if it existed. *h.* Commencement of the Eustachian tube. *j.* Jugular fossa, immediately below the tympanum. *k, k.* Carotid canal, with the artery in outline, to show its course in relation to the tympanum and Eustachian tube. *l.* Portio dura of the seventh pair of nerves, as it would be seen in the terminal part of the aqueduct of Fallopius. *m.* Chorda tympani, leaving the portio dura, and entering a short canal, which opens in the tympanum, at the base of the pyramid. *n.* Grooves for the tympanic plexus.

The *internal wall* of the tympanum (fig. 132) has two orifices of communication with the internal ear; the *fenestra ovalis*, *a*, leading to the vestibule, and the *fenestra rotunda*, *b*, opening into the cochlea. Both these are closed by membrane which prevents the escape of the fluid contained in these inner chambers, and communicates vibrations to it. The fenestra ovalis is likewise occupied by the base of the stapes, one of the chain of ossicles connecting it with the membrana tympani. Between the fenestræ is the *promontory*, *c*, corresponding to the first turn of the cochlea, and furrowed by two or three canals for the nerves which form the *anastomosis of Jacobson*, *n*. Behind the fenestra ovalis is a conical eminence, the *pyramid*, *d*, hollowed, and presenting a small orifice at its summit, which is on a level with the middle of the vestibular fenestra. The pyramid contains the stapedius muscle, the tendon of which emerges at its summit, and runs to the neck of the stapes. This muscle is supplied

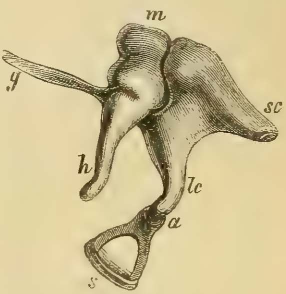
by a twig from the portio dura of the seventh pair. At the base of the pyramid is an aperture through which the chorda tympani, *m*, enters the tympanum. Thence this nerve passes forwards, between the handle of the malleus and the long arm of the incus, and emerges through a canal close to the Glaserian fissure. Above the pyramid an arched prominence, *e*, indicates the course of the aqueductus Fallopii, close to the tympanum; and behind this is the free communication with the mastoid cells, *f*.

The anterior part of the tympanum presents above the canal for the tensor tympani muscle, and below the orifice of the Eustachian tube. The former, *i*, is chiefly formed by a curled plate of bone, the *processes cochleariformis*, *g*, ending in a kind of perforated summit, that some have termed, *anterior pyramid*. This is a little above the fenestra ovalis, and gives passage to the tendon of the tensor tympani, which becomes attached to the short process of the malleus. The *Eustachian tube*, about one inch and a half in length, leads from the tympanum downwards, forwards, and inwards to its orifice in the pharynx, which is seen as a slit with an elevated edge close behind the inferior turbinated bone of the nose (see fig. 106, *t*, p. 8). By its straight, but inclined course, the passage of mucus from the tympanum is facilitated. Its upper extremity for more than half an inch is bony, while in the rest of its extent it is cartilaginous. It dilates at each end, especially the lower, where the cartilage is thickened and everted. It forms a passage for the air in and out of the tympanum. It exists in all animals in which a tympanum is found, but in many, the tubes of opposite sides have a common outlet on the pharynx. External to the opening for the Eustachian tube is the opening for the anterior muscle of the malleus (Glaserian fissure) and that for the escape of the chorda tympani.

The *ossicles of the tympanum* are three, the malleus, the incus, and the stapes (fig. 133). The *malleus* (hammer) has a large extremity above, termed the head, *m*, bounded by a constriction or *neck*, from which the *handle* (manubrium), *h*, passes down, imbedded in the membrana tympani, as already described. Its concavity directed outwards explains the similar inequality of that membrane. The *short process* is a slight conical projection from the neck, which receives the insertion of the tensor tympani muscle: the *slender process* (p. gracilis), *g*, also passes from the neck, but forwards and outwards, to enter the Glaserian fissure. On the back of the head and neck an articulation is formed with the incus. The *incus* (anvil), is shaped not unlike a molar tooth. It articulates with the malleus by the anterior surface or summit of its *body*, and has two processes, a

short and a *long crus:* the former, *sc*, has a backward direction, and projects into the mastoid cells, the latter, *lc*, descends to a level with the fenestra ovalis, bends inwards, and is tipped with a *lenticular process*, to which the head of the stapes is attached, *a*. The *stapes*, or stirrup bone, *s*, is almost sufficiently described by its name. Its construction is truly elegant. It has a *head*, *neck*, *two branches*, and a *base*. The last fits into the fenestra ovalis, to the margin of which it is attached, by membrane, so as to enjoy some freedom of motion. Its neck receives the insertion of the stapedius muscle. The chain of ossicles, now described, stretches across the tympanum by no means in a straight line, and its parts are permitted to enjoy some degree of motion, not merely by the double joint existing between them, but by the mode of their attachment at either end.

Fig. 133.



Ossicles of the left ear articulated, and seen from the outside and below. *m*. Head of the malleus, below which is the constriction, or neck. *g*. Processus gracilis, or long process, at the root of which is the short process. *h*. Manubrium, or handle. *sc*. Short crus; and *lc*, long crus of the incus. The body of this bone is seen articulating with the malleus, and its long crus, through the medium of the orbicular process, here partly concealed, *a*, with the stapes. *s*. Base of the stapes. Magnified three diameters. From Arnold.

These bones are moved by small muscles, two of which are not disputed. These are the *internal muscle of the malleus*, and the *stapedius* muscle. Each of these muscles consists of striped fibres.

The *internal muscle of the malleus*, or *tensor tympani*, occupies the canal above the osseous portion of the Eustachian tube. It is attached in front to the under surface of the petrous bone, and to the cartilage of the Eustachian tube; it proceeds backwards, and ends in a tendon which turns abruptly outwards from the osseous canal in which the muscle is lodged, and is inserted into the short process of the malleus. It draws this part inwards, and thus heightens the tension of the membrana tympani. An *anterior muscle of the malleus*, or *laxator tympani* muscle, is described by many anatomists as passing from the Glaserian fissure to the processus gracilis. The *stapedius muscle* occupies the conical interior of the pyramid; its surface is aponeurotic, its interior fleshy, and it terminates in a small tendon which emerges at the apex of the pyramid, and then passes to be inserted into the neck of the stapes. In contraction it would fix the stapes by pulling its neck backwards. It probably compresses the contents of the vestibule.

Of the Internal Ear, or *Labyrinth.*—This is the potential part

of the organ of hearing, and includes the ultimate distribution of the nerve. It consists of three parts, the vestibule, the semi-circular canals, and the cochlea, all of which, from their delicacy and minuteness of structure, demand careful examination. They are a series of cavities hidden in the hardest part of the petrous bone, communicating on the outside with the tympanum, by the fenestræ ovalis and rotunda already described, and on the inside with the internal auditory canal, which conveys the nerve to them. The very compact bone immediately bounding these cavities, considered apart from the less dense bone which surrounds it, is termed the *osseous labyrinth*, in distinction from a *membranous labyrinth* within.

Of the Osseous Labyrinth.—The singularly complex shape of this part of the organ makes it difficult to describe. 1. The *vestibule* or common central cavity, placed immediately to the inner side of the tympanum, is flattened from side to side, and about a fifth of

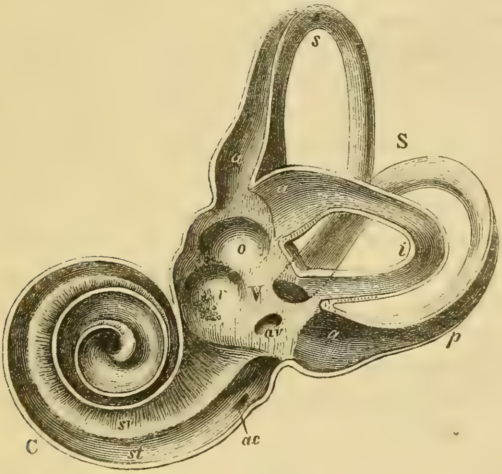
Fig. 134.

Osseous labyrinth of the left side. *o.* Fenestra ovalis, leading into the cavity of the vestibule. From this a bristle, †, is passed into *v v*, the vestibular scala of the cochlea, which is laid open in part by the removal of the outer wall. *r.* Fenestra rotunda, seen almost in profile. Through this a bristle, ‡, is passed into the tympanic scala of the cochlea, *t t*, exposed by the removal of part of the membranous portion of the lamina spiralis. The three semicircular canals are seen, with their extremities entering the vestibule, and one end of each dilated into an ampulla. Magnified 3½ diameters. Partly from Sœmmerring.

an inch in height, as well as from before backwards. The semicircular canals open into it by five orifices behind, the cochlea by a single one in front; on its outer wall is the fenestra ovalis, on its inner several minute holes, including the macula cribrosa for the

entrance of a portion of the auditory nerve from the internal auditory meatus. At the hinder part of the inner wall is the orifice of the aqueductus vestibuli, a fine canal penetrating the vestibule from the posterior surface of the petrous bone, and containing, as some describe, a tubular prolongation of the lining membrane of the vestibule, ending in a minute pouch between two layers of the dura

Fig. 135.



Interior of the osseous labyrinth. V. Vestibule. *a v.* Aqueduct of the vestibule. *o.* Fovea semi-elliptica. *r.* Fovea hemispherica. S. Semicircular canals. *s.* Superior. *p.* Posterior. *i.* Inferior. *a a a.* The ampullar extremity of each. C. Cochlea. *a c.* Aqueduct of the cochlea. *sv.* Osseous zone of the lamina spiralis, above which is the scala vestibuli, communicating with the vestibule. *st.* Scala tympani below the spiral lamina. From Sœmmerring.

mater, within the cranial cavity. Breschet considers this to be an evidence of a continuity once existing between the lining membrane of the cranium, and that of the vestibule, and it is certain that in most fishes the vestibule is a process of the cranial cavity, or separated from it only by a membraniform septum. Whatever other use the aqueduct of the vestibule may serve, it seems, certainly, to convey small vessels to the internal ear. The lower part of the inner wall presents a hemispherical depression (*fovea hemispherica*), and immediately above it, and on the upper wall, another transversely oval and larger (*fovea semi-elliptica*). These are separated by a small *pyramidal eminence.*

2. The *semi-circular canals* are three in number, all opening at both ends into the vestibule, so that there would be six orifices, were not one of the orifices common to two of the canals. The canals are of unequal length, but all describe more than half a circle

and their cavity is not cylindrical, but slightly compressed on the sides, and about a twentieth of an inch in diameter. Each is dilated at one end into an *ampulla*, of more than twice the diameter of the tube, and at the opposite end it opens out slightly on entering the vestibule. Each canal lies in a different plane, the direction of which being constant, should be carefully noticed in relation to their function. The *superior vertical* canal is also *anterior*, and lies across the petrous bone. It forms about two-thirds of a circle, and its extremities are more divergent than those of the others. In the fœtus the concavity of this canal is free, owing to a deficiency in the substance of the petrous bone, and its arch forms a projection within the cranium, even in the adult. The ampulla is on its outer extremity. The *inferior vertical* canal is also *posterior*, and runs parallel to the posterior surface of the petrous bone, and therefore at right angles to the former. The ampulla is at its lower extremity, and its upper end joins the inner end of the former canal, to constitute a common canal an eighth of an inch long, rather wider than those which join to form it, an opening behind and below. The *horizontal* canal is also *inferior*, and shorter than either of the others ; its arch is directed outwards and backwards ; its ampullar extremity is close to that of the superior vertical canal.

3. The *cochlea* is, in shape, very like a common snail-shell. It lies almost horizontally, its apex forwards and outwards, its base marked near the bottom of the internal meatus, by a depression exhibiting a spiral arrangement of pores for the reception of the cochlear division of the auditory nerve. From base to apex extends the irregularly conical *axis*, *modiolus*, or *columella*, which is perforated by numerous branching channels, ascending from the pores just mentioned, and distributing the nervous filaments in regular succession within the spiral cochlear canal which winds around the axis. This *spiral canal* is about an inch and a half in length, if measured along its outer wall, and diminishes gradually in size from the base to the summit of the cochlea, where it ends in a cul de sac. At its commencement it is about one-tenth of an inch in diameter, but at its termination scarcely half that size. At its base it diverges somewhat from the modiolus towards the tympanum and vestibule, and presents three openings. Of these, one, free and oval, enters the vestibule ; another is the fenestra rotunda, communicating with the tympanum in the dry bone, but filled up in the recent state by a proper membrane, the *membrana tympani secundaria ;* the third is the minute orifice of the *aqueductus cochleæ*, a funnel-shaped canal leading to

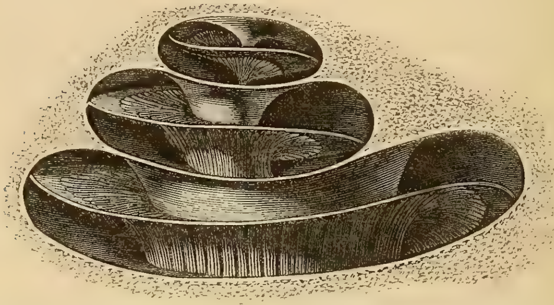
the jugular fossa, and supposed to transmit a small vein. The spiral canal describes about two turns and a half, of which the first, passing round the large base of the modiolus, takes much the widest sweep, so as to encircle most of the second turn. The inner wall of this coiled canal, as has been shown by Ilg, forms the outer wall of the modiolus.

The spiral canal of the cochlea is subdivided into two passages by an osseo-membranous lamina, extended between its modiolar and peripheral wall, and of course taking the same spiral direction as the canal itself. This is the *lamina spiralis*, the fundamental element of the cochlea, on which the nervous tubules are spread out. More than half its breadth on the side of the modiolus is formed by a very brittle osseous process from the modiolus, called the *osseous zone*, enclosing minute channels continuous with those of that part, and transmitting the nerves; its opposite or outer portion is membranous and muscular, and connects the outer thin edge of the osseous zone to the outer wall. The osseous zone commences gradually within the vestibule, and enters the spiral canal between the vestibular and tympanic openings of the cochlea, forming, with the help of the membranous extension, a complete septum between them. The passages, or *scalæ*, into which the spiral lamina divides the canal, correspond, therefore, respectively to those chambers; the upper, towards the apex of the cochlea, *scala vestibuli*, the lower, towards its base, *scala tympani*. These scalæ are, on the whole, pretty equal in size; the vestibular scala is, however, the smaller at the base, the tympanic, near the apex, of the coil; and the latter ceases ere it reaches the summit. At the apex of the cochlea the parts have an arrangement difficult to describe, though easily understood when seen. The axis, no longer hollow, and containing nerves, is reduced to a delicate lamella at about half a turn from the dome-like summit, or *cupola*, formed by the last part of the spiral canal. This lamella, which is the real apex of the modiolus, immediately expands, stretches upwards, and becomes more twisted on itself, so as to include part, or all of the last half turn of the cochlear canal, being termed from its appearance as viewed from below, the *infundibulum*, or funnel. The wide part of this imperfect funnel is directed towards the cupola, with which it blends. It is not open above, but on the side, and it is, in fact, the outside of the last half turn of the canal, projecting into the turn below.

The osseous zone of the spiral lamina ceases with the hollow modiolus at the slender lamella already mentioned, terminating by a small projecting hook (*hamulus*), the concave border of which is

free, and directed towards the lamella, so as to leave an opening or deficiency, the *helicotrema* of Breschet, by which the scalæ tympani and vestibuli communicate. The membranous zone connects the convex border of the hook to the outer wall, and is also con-

Fig. 136.



Cochlea of a new-born infant, opened on the side towards the apex of the petrous bone. It shows the general arrangement of the two scalæ, the lamina spiralis, and the distribution of the cochlear nerve. At the apex is seen the modiolus expanding into the cupola, where the spiral canal terminates in a cul de sac. The helicotrema is not visible in this view. From Arnold.

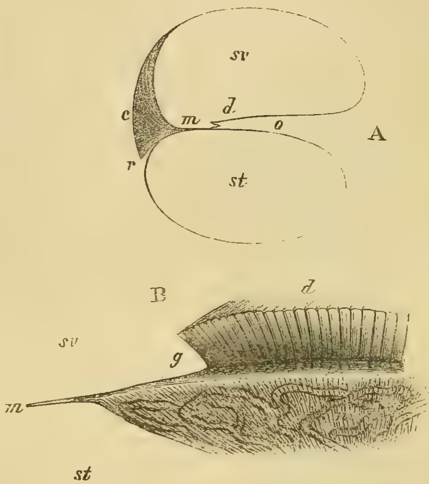
tinued upwards beyond the point of the hook, presenting, however, towards the infundibulum, like the hook itself, a free concave border, contributing to form the orifice of communication.

Such being the form of the osseous labyrinth, we may now proceed to consider the more delicate parts of the organ, and the immediate distribution of the auditory nerves. We must premise that the cavity of the osseous labyrinth is occupied by a limpid fluid, the *perilymph*, so called by De Blainville, from its surrounding, though in the vestibule and semicircular canals only, a hollow membranous apparatus, the *membranous labyrinth*, which latter itself contains a similar fluid, the *endolymph*.

Of the Structure of the Spiral Lamina of the Cochlea.—We shall term the two surfaces of this lamina tympanic and vestibular, as they regard respectively the tympanic or vestibular scala. The *osseous* portion of the spiral lamina extends more than half way from the modiolus towards the outer wall, and is perforated, as already described, by a series of plexiform canals for the transmission of the cochlear nerves; these canals, taken as a whole, lie close to the lower or tympanic surface, and open at or near the margin of this zone. The *vestibular surface* of the osseous zone presents in about the outer fifth of its extent, a remarkable covering, more resembling the texture of cartilage than anything else, but having a peculiar arrangement quite unlike any other with which we are acquainted.

Being uncertain respecting the office of this structure, we shall term it the *denticulate lamina* (figs. 137, and 138), from a beautiful series of teeth, forming its outer margin, which project free into the vestibular scala, and, in the first coil, terminate almost on a level with the margin of the osseous zone, but more within this margin towards the apex of the cochlea. They thus constitute a kind of second margin to the osseous zone, on the vestibular side of the true margin, and having a groove beneath them, which runs along the whole lamina spiralis, in the vestibular scala, immediately above the true margin of the osseous zone. The intervals between the teeth are to be seen on their upper surface, on their free edge, and also within this groove, so that the teeth are wedge-shaped, and their upper and under surfaces, traced from the free edge, recede. The free projecting part, or teeth of the denticulate lamina form less than a fourth of its entire breadth, and in the remainder of its extent it appears to rest on the osseous zone; seen from above, after the osseous zone has been rendered more transparent by weak hydrochloric acid, (fig. 138) rows of clear lines may be traced from the teeth at the convex edge, towards the opposite or concave edge of the lamina. These lines appear to be a structure resembling that of the teeth themselves, and they are separated from one another by rows of clear, highly refracting granules, which render the intervals very distinct. These intervals, as seen in the figure, are more or less sinuous and irregularly branched.

Fig. 137.



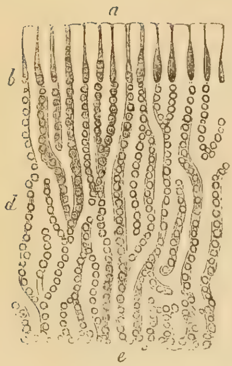
A. Section of the cochlear canal, where the scalæ are equal. *sv*. Scala vestibuli. *st*. Scala tympani. *o*. Osseous zone of lamina spiralis. *d*. Denticulate lamina. *m*. Membranous zone. *c*. Cochlearis muscle. *r*. Osseous rim of the groove of the cochlearis.

B. Margin of osseous zone, more magnified. *sv*. Scala vestibuli. *st*. Scala tympani. *g*. Groove, between *d*, denticulate lamina, and *m*, membranous zone springing from edge of the osseous zone. *n*. Cochlear nerves and capillaries, distributed on the typanic surface of the osseous zone.

The denticulate lamina, thus placed on the vestibular surface of the osseous zone, is above, and at some distance from the plexus of the cochlear nerves, which lies near its tympanic surface. The vestibular

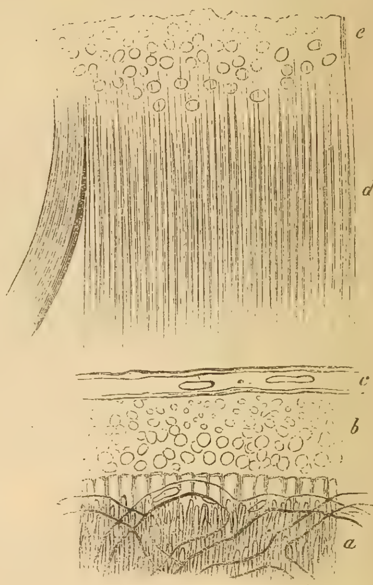
surface of the osseous zone, including the denticulate lamina, is convex, rising from the free series of teeth towards the modiolus.

Fig. 138.



Denticulate lamina of the osseous zone of the lamina spiralis, seen on the vestibular surface. *a.* Free edge of the teeth, which are separated by fissures as far as the line *b.* The clear tracts, with intervening rows of globules, are seen at *d, e.* Margin towards the axis of the cochlea. From the sheep. Magnified 100 diameters.

Fig. 139.



Tympanic surface of a portion of the lamina spiralis of the cat. *a.* Termination of the cochlear nerves at the border of the osseous zone, with capillaries ramifying over them. *b.* Inner clear belt of the membranous zone. *c.* Marginal capillary on the tympanic surface. *d.* Pectinate portion of the membranous zone. The half-detached fragment on the opposite edge shows its mode of tearing. *e.* Outer clear belt of membranous zone, torn from the cochlearis muscle. Magnified 300 diameters.

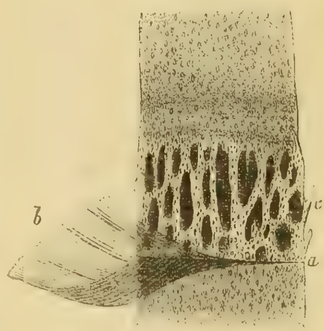
In the groove already mentioned there is a series of elongated bodies, not unlike columnar epithelium, in which the nuclei are very faint. These bodies are thick and cubical at one end, and taper much towards the other. They are united in a row; and it is possible they may have some analogy to the club-shaped bodies of Jacob's membrane. We can assign them no use.

Continuous with the thin margin of the osseous zone is the *membranous zone.* This is a transparent glassy lamina, having some resemblance to the elastic laminæ of the cornea, and the capsule of the lens. A narrow belt of it next the osseous zone is smooth, and exhibits no internal structure, while in the rest of its width it is marked by a number of very minute straight lines, radiating outwards from the side of the modiolus. These lines are very delicate at their commencement, become more strongly

marked in the middle, and are again fainter ere they cease, which they do at a curved line on the opposite side. Beyond this the membranous zone is again clear, and homogeneous, and receives the insertion of the cochlearis muscle. The *inner clear belt* of the membranous zone is little affected by acids. It seems hard and brittle. The middle or *pectinate portion* is more flexible, and tears in the direction of the lines. The *outer clear belt* is swollen, and partially destroyed by the action of acetic acid. Along the inner clear belt, and on its tympanic surface, runs a single, sometimes branched vessel, which would be most correctly called a capacious capillary, as it resembles the capillaries in the texture of its wall, but exceeds them in size. It is the only vessel supplied to the membranous zone, and seems to be thus regularly placed, that it may not mar the perfection of the part as a recipient and propagator of sonorous vibrations.

Of the Cochlearis Muscle.—At its outer or convex margin, the membranous zone is connected to the outer wall by a semi-transparent structure. This gelatinous looking tissue was observed by Breschet, and is indeed very obvious on opening the cochlea; but we are not aware of any one having hinted at what we regard to be its real nature. The outer wall of the cochlear canal presents a groove, ascending the entire coil, opposite the osseous zone of the lamina spiralis, and formed principally by a rim of bone, which, in section, looks like a spur (fig. 137, *r*), projecting from the tympanic margin of the groove, the opposite margin being very slightly or not at all marked. This groove diminishes in size towards the apex of the cochlea. It gives attachment to the structure in question, by means of a firm dense film of tissue, having a fibrous character, and the fibres of which run lengthwise in the groove, and are intimately united to it, especially along the projecting rim. From this *cochlear ligament*, the cochlearis muscle passes to the margin of the membranous zone, filling the groove, and projecting into the canal, so as to assist in dividing the tympanic and vestibular scalæ from one another, and thus forming in fact the most external, or the *muscular zone* of the spiral lamina.

Fig. 140.



Inner view of cochlearis muscle of the sheep. *a*. Line of attachment of membranous zone of lamina spiralis, of which a portion, *b*, remains attached. The surface below this line is in the scala tympani; the surface above, in the scala vestibuli. *c*. Projecting columns, with intervening recesses, in the vestibular part of the cochlearis muscle.

Thus the cochlear muscle is broad at its origin from the groove of bone, and slopes above and below to the thin margin in which it terminates, so that its section is triangular, and it presents three surfaces, one towards the groove of bone, and one to each of the scalæ. The surface towards the vestibular scala is much wider than that towards the tympanic scala, and presents, in a band running parallel to and at a short distance from the margin of the membranous zone, a series of arched vertical pillars, with intervening recesses, much resembling the arrangement of the musculi pectinati of the heart (fig. 140, *c*). These lead to and terminate in the outer clear belt of the membranous zone, which forms a kind of tendon to the muscle. This entire arrangement is almost sufficient of itself to determine the muscular nature of the structure. If its fibres were of the striped variety no doubt would remain; but its mass, evidently fibrous, is loaded with nuclei, and filled with capillaries, following the direction of the fibres, and in almost all respects it has the closest similarity to the ciliary muscle of the eye. The nuclei diminish in number as the fibres end in the tendinous part; and they are made much more evident by the addition of acetic acid. The action of the muscle must be that of making tense the membranous portion of the lamina spiralis, and so perhaps of adjusting it to the modifications of sound. As the ciliary muscle, though of the unstriped variety, adjusts the transparent media of the eye to distinct vision at different distances under the guidance of the will, so it is not impossible that the cochlear muscle may have a voluntary adjusting power, though its precise mode of action as a part of an acoustic apparatus may still remain obscure. On the whole, however, we are more disposed to regard this very interesting structure as having a preservative office, as being placed there to defend the cochlear nerves from undue vibrations of sound, in a way analogous to that in which the iris protects the retina from excessive light. These nerves are acted on principally by vibrations brought through the osseous part of the cochlea, and it is probable that the arrangement of the scalæ is one designed to allow of protective movements of the lamina spiralis by muscular action, under a stimulus reflected from impressions on the auditory nerve.

The capillaries of the ciliary muscle are derived from vessels meandering over the walls of the scalæ before entering it, and those from above and below do not anastomose across the line of attachment of the membranous zone, thus indicating that the continuation of this zone enters as a plane of tendon into the interior of the muscle, dividing it into two parts, and receiving the fibres in succession.

The scalæ of the cochlea are lined with a nucleated membrane, or epithelium, which is very delicate and easily detached, usually more easily seen in the vestibular than in the tympanic scala, and in many animals containing scattered pigment.

Of the cochlear nerves.—These enter from the internal auditory meatus through the spirally-arranged orifices at the base of the modiolus, and turn over in succession into the canals hollowed in the osseous zone of the spiral lamina, close to its tympanic surface. In this distribution the nervous bundles subdivide and reunite again and again, forming a plexus with elongated meshes, the general radiating arrangement of which can be readily seen through the substance of the bone when it has been steeped in diluted hydrochloric acid (fig. 141). Towards the border of the osseous zone the bundles of the plexus are smaller and more closely set, so as at length almost to form a thin uniform layer of nervous tubules. Beyond the border, and partially on or in the inner transparent belt of the membranous zone, these tubules arrange themselves more or less evidently into small sets, which advance a short distance and then terminate much on the same level. These terminal sets of tubules are cone-shaped, coming to a kind of point ere they cease. The white substance of Schwann exists in them throughout, but is thrown into varicosities and broken with extreme facility, and they are interspersed with nuclei, so that it is very difficult to discover the precise disposition of the individual tubules (fig. 139, *a*). They seem to cease one after another, thus causing the set to taper; and at least it appears certain that evidence of loopings, such as have been described by some, is wanting. In the cochlea of the bird, however, we have seen at one end a plexiform arrangement of nucleated fibres ending in loops; but this is a peculiar structure.

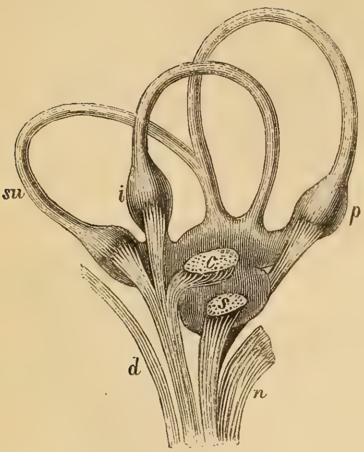
Fig. 141.

Plexiform arrangement of the cochlear nerves seen in the basal coil of the lamina spiralis, treated with hydrochloric acid. There are no ganglion globules in this plexus, which consists of tubular fibres. *a.* Twig of cochlear nerve in the modiolus, its fibres diverging and reuniting in *b*, a band in the plexus taking a direction parallel to the zones. From this other twigs radiate, and again and again branch and unite as far as the margin of the osseous zone *c*, where they terminate. From the sheep. Magnified 30 diam.

The capillaries of the osseous zone are most abundant on the tympanic scala, in connexion with the nerves now mentioned, and form loops near the margin, with here and there an inosculation with the large marginal capillary already mentioned.

Of the membranous labyrinth (fig. 142). This has the same general shape as the bony cavities in which it lies, but is consider-

Fig. 142.



Membranous labyrinth of the left side, with its nerves and otoliths:—*su.* Superior semicircular canal, with the ampulla and its nerve at one end, and the other end joined by *p*, the posterior canal, to form the *tubulus communis.* *i.* Inferior, or horizontal canal, with the ampulla and its nerve at one end, and the other entering the utriculus separately. *c.* Powdery otolith seen through the translucent wall of the common sinus, or utriculus, with the nerves distributed to it. *s.* Powdery otolith of the sacculus seen with its nerve, in a similar way. *n.* Cochlear division of the auditory nerve cut off where it enters the cochlea. *d. Portio dura* of the seventh pair leaving the auditory nerve, or *portio mollis,* to enter the aqueduct of Fallopius. Magnified. From Breschet.

ably smaller, so that the perilymph intervenes in some quantity, except where the nerves passing to it confine it in close contact with the osseous wall. Its vestibular portion consists of two sacs, viz.: a principal one of transversely oval figure and compressed laterally, called the *utriculus* or *common sinus*, occupying the upper and back part of the cavity, in contact with the fovea semi-elliptica, and beneath this a smaller and more globular one, the *sacculus*, lying in the fovea hemispherica, near the orifice of the vestibular scala of the cochlea, and probably communicating with the utriculus.

The *membranous semicircular canals* have the same names, shape, and arrangement as the osseous canals which enclose them, but are only a third of the diameter of the latter. As the osseous canals open into the vestibule, so the membranous ones open at both ends into the utriculus—there being, however, a constricted neck between this sac and the ampullated extremity of each canal. The auditory nerve sends branches to the utriculus, to the sacculus, and to the ampulla of each membranous canal. These nerves enter the vestibule by the minute apertures before described, and tie down, as it were, both the utriculus and sacculus to the osseous wall at those points, the membrane being much thicker and more rigid where the nerves join it. The branches to the ampullæ of the superior vertical and the horizontal semicircular canals enter the vestibule with the utricular nerve, and then cross to their destinations, while that to the ampulla of the posterior vertical canal traverses the posterior wall of the cavity and opens directly into the ampulla.

The wall of the membranous labyrinth is translucent, flexible, and tough. When withdrawn from its bed and examined, it appears to present three coats, an outer, middle, and internal. The outer is loose, easily detached, somewhat flocculent, and contains more or

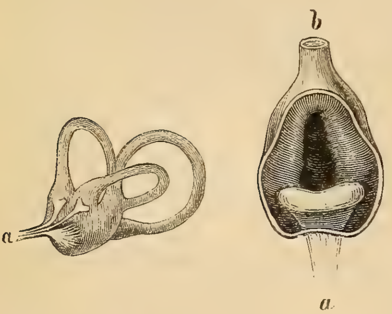
less colouring matter disposed in irregular cells, exactly resembling those figured at page 22, from the outer surface of the choroid coat of the eye. We have not found a true epithelium on this surface. The middle is the proper coat, and seems more allied to cartilage than to any other tissue; its limits are well marked, it is transparent, and exhibits in parts a longitudinal fibrillation: treated with acetic acid, it presents numerous corpuscles or cell-nuclei. Where it is thinnest it has a near resemblance to the hyaloid membrane of the eye. The internal coat is composed of nucleated particles closely apposed and but slightly adherent; the nuclei are often saucer-shaped, and when seen edgeways have the uncommon appearance of a crescent. They easily become detached and fall into the endolymph. Minute arteries and veins, derived chiefly from a branch of the basilar accompanying the auditory nerve, enter the vestibule from the internal meatus, and ramify on the exterior of the membranous labyrinth, apparently bathed in the perilymph. A beautiful network of capillaries, forcibly reminding the observer of that belonging to the retina, is spread out on the outer surface and in the substance of the proper coat. These vessels have the simple homogeneous wall, interspersed here and there with cell-nuclei, that characterises the capillary channels in many other situations. There is an abundant network of capillaries in the interior of the utriculus and sacculus about the terminal distribution of the nerves, which evinces the activity of the function of these parts.

The membranous labyrinth, or its simple representative the auditory sac, contains, in all animals, either solid or pulverulent calcareous matter, in connexion with the termination of the vestibular nerves. This has been called by Breschet *otolith*, or *ear-stone*, when solid, as in the osseous fishes, and *otoconia*, or *ear-powder*, when in the form of minute crystalline grains, as in mammalia, birds, and reptiles, but the former term may be conveniently employed to designate both varieties. In the mammalia, including man, it is found accumulated in small masses about the termination of the nerves, both in the utriculus and sacculus, and we have found it also sparingly scattered in the cells lining the ampullæ and semicircular canals. In the vestibular sacs, it appears to be entangled in a mesh of very delicate branched fibrous tissue, in connexion with the wall, and it is most probably held in place by cells within which, according to Krieger,* its particles are deposited. It has a regular arrangement, and is not free to change its place in the endolymph. Otoliths consist always of carbonate of lime.

* De Otolithis, Berol. 1840.

Of the vestibular nerves.—In consequence of the thickness of the wall of the membranous labyrinth where the nerves enter, and the presence there of the calcareous and fibrous matter, it is not easy to ascertain with certainty the precise manner in which the nerves terminate. In the utricle and saccule, they appear to spread out from one another as they enter, and then to pass, some to mingle with the calcareous powder, others to radiate for a small extent on the inner surface of the wall of the cavity, where they come into connexion with a layer of dark and closely-set nucleated cells, and presently lose their white substance. We have seen a fibrous film on the inner surface of these parts which we are disposed to consider as formed, like the inner surface of the retina, by the union of the axis-cylinders of the nerve-tubes, but confirmatory observations are required. Those that traverse the calcareous clusters have appeared to us, in the most lucid views we have succeeded in obtaining, to terminate by free, pointed extremities, without losing their white substance. In the frog this has been evident enough.

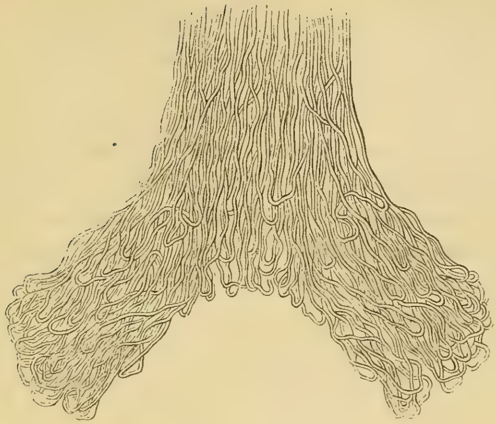
Fig. 143.



View of the nerves going to the membranous labyrinth:—*a*. Branch to the ampulla of one of the semicircular canals. It is seen perforating the wall and expanding transversely within. *b*. Semicircular canal cut across. From Steifensand.

The nervous twigs belonging to the semicircular canals do not seem to advance beyond the ampullæ, in which they have a remarkable distribution, entering them, as Steifensand has well shown, by a transverse or forked groove on their concave side, and which reaches about a third round. Within this, the nerve projects so as to form a sort of transverse bulge within the ampulla. Their precise termination can be best seem in the osseous fishes, and has been described by Wagner to be looplike, as will be apparent from the adjoined figure. We believe we have seen this mode of termination, though certainly never so plainly as the figure given by this excellent author would indicate; and we may add that we have found free extremities to the nerve-tubes, as well as loopings, in the ampullæ of the cod. The difficulty in these cases of ascertaining the exact truth arises from the curves formed by the nerve-tubes in proceeding to their destination, and which are liable to be mistaken for terminal loopings.

Fig. 144.



Termination of the nerve in the ampulla of a Ray, highly magnified. (From Wagner.)

Of the Auditory Nerve.—The *portio mollis* of the seventh pair has its origin from the medulla oblongata by two roots. One penetrates to the central part of the medulla oblongata in the same way, and following the same direction, as the portio dura, but passing to a much greater depth into its substance. The other winds round the corpus restiforme, not penetrating it, but simply adhering to its surface, until it reaches the floor of the fourth ventricle, where it connects itself with the olivary columns, and in many instances is evidently continuous with the white striæ on either side of the calamus scriptorius, which for that reason have been very generally regarded as fascicles of origin of the portio mollis.

The portio mollis, when contrasted with the other nerves of the medulla oblongata, is remarkable for its delicacy of structure, a character which had attracted the attention of the older anatomists, and by reason of which they had given the nerve the appellation "mollis." It has but a very delicate neurilemma, and its fascicles are loosely held together; it seems strictly a direct prolongation of the white matter of the brain.

The portio mollis enters the internal auditory foramen, and there forms a connexion with the portio dura, by means of a few fascicles of fibres which constitute the "portio intermedia" of Wrisberg. It is difficult to say whether this consists of fibres proceeding from the auditory to the facial nerve, or from the latter to the former. It is most reasonable to suppose that the muscular nerve (the facial)

sends some filaments into the labyrinth to the blood vessels, and to the muscular structure of that portion of the ear.

At the bottom of the meatus, the portio mollis divides into two branches, one to the vestibule and semicircular canals, the other to the cochlea.

The vestibular nerve divides into three branches:—the largest is uppermost, and penetrates the depression which is immediately behind the orifice of the aqueduct of Fallopius to be distributed to the utriculus, and to the ampullæ of the superior vertical and the horizontal semicircular canal. The second branch of the vestibular nerve is distributed to the sacculus, and the third to the posterior vertical semicircular canal.

The cochlear nerve penetrates the funnel-shaped depression at the bottom of the auditory canal, and proceeds from it through the numerous foramina, by which its wall is pierced, in a spiral manner, to the lamina spiralis of the cochlea.

The mode of distribution of these nerves has been already described.

The labyrinth receives nerves from no other source but the portio mollis, unless we suppose the portio intermedia to consist of filaments from the facial which accompany the ramifications of that nerve into that part of the ear.

That the *portio mollis* is the nerve of hearing is abundantly proved by the following arguments:—1. The distribution of the nerve to the internal ear, to which no other nerve of any importance is distributed. 2. Its softness of texture and cerebriform character distinguish it from ordinary nerves of sensation or motion. 3. Diseased states of it or of parts immediately near to its origin affect the sense of hearing, whilst a paralytic state of the portio dura or of the fifth does not affect the sense.

Of the Nervous Apparatus accessory to the Organ of Hearing.—Besides the auditory nerve there are others which influence the auditory apparatus. These are branches of the portio dura, branches of the nerve of Jacobson, from the glossopharyngeal, and from the otic ganglion.

These nerves present a striking analogy with those which are distributed to the eye.

The tympanum receives branches from the facial, and glossopharyngeal, and probably from the sympathetic.

The facial in its passage through the aqueduct of Fallopius, gives off the chorda tympani, which, however, seems to have no physiological connexion with the tympanum or its contents. The stapedius

muscle receives a branch from the facial nerve. The anastomosis of Jacobson results from the subdivision of the tympanic branch of the glossopharyngeal nerve, which enters the cavity of the tympanum below, and passing over the promontory gives off branches to the membranes of the fenestræ, and Eustachian tube, and to the otic ganglion.

A branch is described by Arnold as proceeding from the otic ganglion to the tensor tympani muscle.

The external ear is supplied by the facial nerve as regards its muscular apparatus, and by the fifth pair as regards its sentient surfaces.

The influence of the facial nerve upon the muscular apparatus of the organ of hearing, whether tympanic or labyrinthic, is similar to that of the third nerve upon the muscles of the eyeball, or upon the iris and ciliary muscle. And it seems probable that while volition can exercise a certain influence upon the muscular apparatus of hearing, that apparatus may likewise be excited to action through the physical stimulus of sound affecting the auditory nerve, which re-acting upon the portio dura excites its fibres to a degree proportionate to the intensity of the sound; as the stimulus of light affecting the optic nerve re-acts upon the iris.

We shall now proceed to inquire into the office of each part of the complex organ of hearing.*

* The following points respecting the laws of sound should be borne in mind in considering the offices of the various parts of that complex acoustic apparatus, the human ear.

1. Any irregular impulse communicated to the air will produce a *noise:* a succession of impulses occurring at exactly equal intervals of time, and exactly similar in duration and intensity, constitutes a *musical sound.*

2. The frequency of repetition necessary for the production of a continued sound from single impulses is, probably, generally not less than sixteen times in a second, but Savart thinks that some ears may distinguish a sound resulting from only ten or eight vibrations in a second. On the other hand, sounds are audible which consist of 24,000 vibrations in a second.

3. Sound may be propagated or conducted by air, gases, liquids and solids, with various degrees of rapidity.

4. Sound travels through air at the temperature of 62° Fahr. at the rate of 1125 feet in a second.

5. Sound is incapable of transmission through a vacuum.

6. The propagation of sound is the more effectively performed as the medium of transmission is more dense. Rarefied air, gases of low density, and soft solids, are less perfect conductors of sound than much denser materials of the same kind.

7. We distinguish in sounds, 1, the *pitch;* 2, the *intensity* or *loudness;* 3, the *quality* or *timbre.*

The pitch of the sound depends on the rapidity with which the vibrations succeed

It is necessary for the reader to bear in mind that the organ of hearing may be affected in two ways: first, through the external ear, and secondly, through the bones of the head. Every person must have noticed the difference in the sound of the ticking of a watch if it be held near the ear but not in contact with it, and if it be held between the teeth. The waning note of the vibrating tuning-fork seems revived when the stem of the fork is brought in contact with the teeth or with any part of the head. These differences are due to the difference of the medium through which the sonorous undulations are made to affect the auditory nerve. In the former instance, hearing is excited through the external ear, when the watch is held near that part, and through the bones of the head, when the watch is brought into contact with the teeth. And in the example of the tuning-fork, the sound appears to revive when it is made to affect the nerve through a medium (the bones of the head) which more readily vibrates in unison with the most delicate oscillations of the sounding body.

1. *Of the External Ear.*—The external ear consists of two parts, the *auricle*, and the *meatus auditorius externus.* The complete developement of the former is found only in mammalia, in which class it exists pretty generally; with, however, considerable diversity of

each other, and any two sounds produced by the same number of vibrations or impulses in the same time, are said to be in unison.

The loudness or intensity depends upon the violence and extent of the primitive impulse.

The quality is supposed by Herschel to depend on the greater or less abruptness of the impulses; or generally on the law which regulates the excursions of the molecules originally set in motion.

8. The velocity with which sound travels is, however, quite independent of its intensity or of its tone; sounds of every pitch, and of every quality, travel with the same speed through the same medium, as is proved by the fact, that distance does not destroy the harmony of a rapid piece of music played by a band.

9. Water propagates sound with much greater velocity than air does. Colladon concludes, from numerous observations, that the velocity of sound in water, at 40° Fahr., was at the rate of 4708 feet in a second.

10. According to Biot, cast-iron propagates sound at the rate 11,090 feet in a second.

11. Sonorous undulations in passing from one medium to another always experience a partial reflexion, and when they encounter a fixed obstacle, they are almost wholly reflected. The reflexion of sound occurs according to the same law which regulates the reflexion of light,—namely, the angle of reflexion is equal to the angle of incidence.

12. The phenomena of echoes result from the reflexion of sound from any prominent object.

form, varying from what appears to be little more than a mere cartilaginous lamella with a few irregularities upon its surface, enjoying scarcely any motion, to an elongated funnel-shaped ear-trumpet very moveable, and completely under the control of numerous large muscles. Man and the quadrumana are at one extremity of this scale ; the solipeds, the ruminants, and the bats at the other.

That the auricle performs the office of an acoustic instrument to collect and reinforce the sounds which fall upon it, cannot be doubted in those cases in which it is large and fully developed, as in the horse, ass, &c. These animals employ it as we might expect such an instrument would be used; the open part is directed towards the quarter whence the sound comes, and continues so directed as long as the animal appears to listen.

Savart's experiments illustrate the manner in which an instrument like the external ear may contribute to the propagation of sound to the internal ear. When a thin membrane is stretched in a horizontal direction over the mouth of a glass or other hollow vessel, it may be made to vibrate by holding near it a glass thrown into vibration by passing a violin bow across it. The vibrations of the paper are easily demonstrated by the movements of particles of fine sand, or lycopodium powder strewed upon it. The sand arranges itself into certain very definite figures, the shape of which is determined by the position of the lines of repose, or *nodal lines*, over which the sand accumulates. These phenomena may be shown in the membrana tympani itself, by scattering a little sand upon it, the osseous meatus having been previously cut away. When the vibrating glass is brought near to it, the movement of the particles of sand affords sufficient evidence of the vibration excited in the tympanic membrane, but owing to the slight extent of the membrane it is impossible to determine the existence of any nodal line.

Savart imitated the tympanic membrane, and the external auditory apparatus by a hollow cone of paste-board ; across the narrow extremity some thin paper was stretched. When the vibrating glass was brought near to the narrow end, movements of a slight kind were excited in the paper, but when the glass was brought to the wide extremity of the cone, much more extensive movements were excited in the paper; although now the glass was much more distant from the paper than previously.

This result might have been due chiefly to one of two causes, namely, either to the concentration of the sonorous undulations by the walls of the cone, or to the excitation of vibrations in the walls of the tube, which would be propagated directly to the paper; and

Savart showed by the following simple experiment that the latter cause was obviously the most effective. He prepared a second conical tube open at both ends, and having placed the narrow end of this tube very near the paper on the former one, but not *in contact with it*, he found that vibrations were excited on the paper by bringing the vibrating glass near to the wide end of the second tube, but that these vibrations were not nearly so extensive as when the glass was brought near to the wide extremity of the tube with which the paper was connected.

Hence Savart inferred that the external ear and meatus were parts adapted to enter into vibrations in unison with those of the air, or of any liquid or solid vibrating medium which might be brought in contact with the auricle; and he suggested that the latter part, in the human subject, by the variety of direction and inclination of its surfaces, could always present to the air a certain number of parts whose direction is at right angles with that of the molecular movement of that fluid, and therefore in the most favourable circumstances for entering into vibration with it.

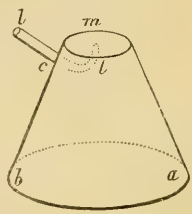
We get a general notion of the value of the external part of the auditory apparatus in collecting and directing the sonorous undulations, from the assistance often derived in hearing by placing the hand behind the external ear, so as to increase its concavity; and by the dulness of hearing, which it is said follows the loss of the auricle. Kerner states that the loss of the auricle is followed by the greatest dulness of hearing in those animals in which the osseous meatus is wanting. In a cat from which the right ear was cut away close to the skull, after the wound had healed without any stoppage of the meatus, there was a remarkable disposition always to keep the head turned so as to be ready to receive sounds with the left ear, and this continued even after the left tympanic membrane was perforated, the right remaining whole; and when the left ear was stopped, (although the right tympanic membrane was sound, and the only injury on that side was the removal of the auricle) a total deafness was manifested except to the loudest and clearest sounds.

The Tympanum and its Contents.—We have already stated that Savart had demonstrated experimentally upon the membrana tympani itself, that that membrane can be thrown into vibrations by undulations of the air excited by a sonorous body. In a second experiment, the cavity of the tympanum was opened, so as to expose the ossicles of the ear and their muscles; and it was observed that when the internus mallei muscle acted and rendered the mem-

brane tense, it was much more difficult to produce manifest movements in the grains of sand; thus affording much reason to suppose that the tensor tympani muscle is analogous in its use to the iris, and destined to protect the organ from too strong impressions. These experiments can be best tried on the membrana tympani of the calf.

In imitation of the mechanism by which the tension of the membrana tympani is effected, and with a view to determine more decisively the effects produced by variation of the tension of that membrane, Savart constructed a conical tube (fig. 145), with its apex truncated and covered by a layer of very thin paper, *m*, which was glued to the edge of the opening. A little wooden lever, *l*, *l*, introduced through an opening in the side of the tube, and resting on the lower margin of this opening, *c*, as a fulcrum, was used to vary the tension of the membrane, one of its extremities being applied to the under surface of the membrane. By depressing the extremity of the lever external to the tube, the inner one is raised, and thus the membrane stretched to a greater or less degree, according to the force used; on the other hand, by elevating the outer extremity, the inner one is separated from the membrane, which is accordingly restored to its original tension. This little lever is an imitation of the handle of the malleus, which, under the influence of its muscles, causes the variation in the tension of the membrana tympani. The artificial tympanic membrane having been then covered with a layer of sand, it was found that, under the influence of a vibrating glass, used as in the former experiments, a manifest difference was produced in the movements of the grains of sand, by increasing the tension of the paper; the greater the tension, the less the height to which the grains of sand were raised; and these movements were most extensive when the lever was withdrawn from contact, and the membrane left to itself.

Fig. 145.



From these experiments Savart concludes that the membrana tympani may be considered as a body thrown into vibration by the air, and always executing vibrations equal in number to those of the sonorous body which excites the oscillations of the air. But what is the condition of the ossicles of the tympanum whilst the membrane is thus in vibration? The result of the following experiment affords a clue to the answer to this question. To a membrane stretched over a vessel, as in fig. 146, a piece of wood, *a*, *b*, uniform

in thickness is attached, so that the adherent part shall extend from the circumference to the centre of the membrane, while the free portion may project beyond the circumference. When a vibrating glass is brought near this membrane, very regular figures are produced, modified, however, by the adhesion of the piece of wood, and the vibrations of the membrane, are communicated to the wood, on which likewise regular figures may be produced. The more extensive the membrane, the longer and thicker may be the piece of wood in which it can excite oscillations, and Savart states that, with

Fig. 146.

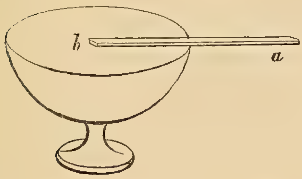
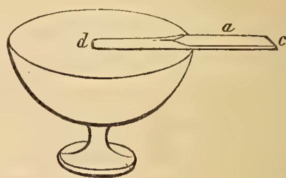


Fig. 147.

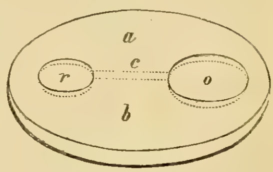


membranes of a considerable diameter, he has produced regular vibrations in rods of glass of large dimensions. The oscillations of the piece of wood are much more distinct when the adherent portion is thinned down, as in *c*, *d*, fig. 147, by which it becomes more completely identified with the membrane; the oscillations of this latter are communicated directly to the thinned portion of the wood, and thence propagated to the thick portion, *a*: sand spread upon *a* will exhibit active movements, and will indicate very distinct nodal lines. Hence it may be inferred that the malleus participates in the oscillations of the tympanic membrane: and these vibrations must be propagated to the incus and stapes, and thus to the membrane of the fenestra ovalis. The chain of ossicles then evidently performs the office of a conductor of oscillations from the membrana tympani to the membrane of the fenestra ovalis; but the malleus likewise has the important function under the influence of its muscles of regulating the tension of the tympanic membrane; and to allow of the changes in the position of this bone necessary for that purpose, we find it articulated with the incus by a distinct diarthrodial joint, and between this latter bone again and the stapes there exists another and a similar joint. This mobility then of the chain of bones, and the muscular apparatus of the malleus and stapes have obvious reference to the regulation of the tension of the membrane of the tympanum as well as of that of the fenestra ovalis.

We have already seen how the muscle of the malleus regulates the membrana tympani, increases its tension, and thus limits the extent

of the excursions of its vibrations. The contraction of the stapedius muscle causes the base of the stapes to compress the membrane of the fenestra ovalis to a greater or less extent, so that the degree of tension of that membrane depends on the condition of this muscle. Compression exerted upon the membrane of the fenestra ovalis extends to the perilymph and through it is propagated to the membrane of the fenestra rotunda, and in this way the same apparatus which regulates the tension of the membrane of the fenestra ovalis performs that office for that of the fenestra rotunda, and Savart has devised an apparatus which very prettily illustrates the manner in which this may take place. In a disc of wood (*a*, *b*, fig. 148) of sufficient thickness, he hollows out two cavities, *o* and *r*, which communicate at their bottoms with each other by a narrow canal (*c*) hollowed in the wood, but not open on its surface; a thin membrane is extended over each of the cavities. Thus, the air contained in these cavities may pass easily from one to the other, and may always maintain the same degree of elastic tension in both. If a vibrating glass be brought near the membrane *r*, covered with a layer of sand, it will be found to enter freely into vibration, as evinced by the active movements of the grains of sand. If, now, pressure be made on *o* with the finger, *r* will become convex in proportion as *o* is rendered concave by the pressure, and when in this convex state, the movements of the sand upon it will be much less considerable than before, presenting an effect precisely similar to that produced on the tympanic membrane by an increase of tension. Thus, the extent of the excursions of the vibrations of the membrane *r*, is limited by the pressure exerted upon *o*, and as the membranes of the two fenestræ are related to each other in an analogous manner, we may argue that pressure upon the membrane of the fenestra ovalis, will occasion tension of that of the fenestra rotunda, thereby limiting the extent of the excursions of its vibrations.*

Fig. 148.



Moreover it appears, upon reference to the anatomy of these parts, that the only muscles which have been satisfactorily demonstrated are *tensors* of the tympanum; and that at whichever extremity of the chain of ossicles muscular effort be first exerted, a corresponding effect will be produced at the other; that when the stapedius muscle acts, the malleus is thrown into a position favourable to the

* All these experiments have been frequently repeated and exhibited by us, with the same results as those stated in the text.

tension of the membrana tympani, and, on the other hand, the contraction of the internus mallei depresses the stapes, and consequently increases the tension of the membranes of the two fenestræ. The cessation of muscular action restores all three membranes to their original laxity, nor does it appear that they admit of any further degree of relaxation through the influence of any vital process. The incus forms a bond of union between the two other bones, and its motions depend entirely upon theirs in consequence of its articulation with both, while from the fixedness of its connexion with the mastoid cells, as well as from its intermediate position and want of muscular attachment, its motions must obviously be much more limited than those of the other bones. Its use seems to be to complete the chain in such a manner, that by reason of its double articulation with the malleus on the one hand and the stapes on the other, the tension of the tympanic membranes may be regulated without any sudden or violent motion, which could scarcely be avoided were the conductor between the membranes of the tympanum and fenestra ovalis but one piece of bone.

The mobility of the tympanic bones has, however, a further use, as Müller suggests; namely, to favour the oscillations of the membrana tympani, by allowing the approximation of the two extremities of the chain of bones. And this opinion is strengthened by the facts of comparative anatomy, for the ossicles have moveable articulations in the frog, as in man, although they have no muscles attached to them.

The addition of a cavity filled with air outside the labyrinth has a twofold use. First, to preserve uniformity of temperature in the air immediately in contact with the fenestral membranes. Were these membranes situate on the exterior of the head, and exposed to the surrounding atmosphere, they would be constantly undergoing changes in their elastic state, under the influence of atmospheric vicissitudes. The air which accumulates in the tympanum and mastoid cells, finds its way into them only through the Eustachian tubes, and as it does not readily change its position, it is well placed for maintaining a temperature equal to that of the body. Secondly, the action of the chain of ossicles as conductors is materially enhanced by their being completely surrounded by air. The insulation of a solid body by a different medium renders it a better propagator of sound; for the surrounding medium will obviate the dispersion of sound, and will favour its retention in the solid conductor.

It results from Savart's experiments, that tension of the mem-

brana tympani is unfavourable generally to the propagation of sounds, especially of those of a low pitch. By rendering the membrana tympani tense in one's own person, the correctness of this statement may be readily ascertained. In blowing the nose forcibly air is forced into the tympanum, and its membrane is rendered convex and tense, and every one must have experienced the temporary deafness which remains after such an effort. The tympanic membrane may also be rendered tense by forced inspiration, the nose and mouth being kept shut. Under these circumstances the tympanic cavity is exhausted, and the membrane rendered tense by the pressure of the external air.

In descending in the diving-bell, the membrane of the tympanum is rendered painfully tense by the increased pressure of the air, and the want of counter-pressure from within. This tension may be so great as even to cause rupture of the tympanic membrane in some cases, but it may be obviated by acts of swallowing, during which the external air is driven into the tympana along the Eustachian tubes. During the tense state of the membrane hearing is impaired; M. Colladon found that the voices of his companions and of himself were not so distinctly heard.

Dr. Wollaston performed many experiments upon the effects of tension of the membrana tympani, and he found that deafness to grave notes was always induced, which, as most ordinary sounds are of a low pitch, is tantamount to a general deafness. Shrill sounds, however, are best heard when the tympanic membrane is tense. Müller remarks, und we have frequently made the same observation, that the dull rumbling sound of carriages passing over a bridge, or of the firing of cannon, or of the beating of drums at a distance, ceases to be heard immediately on the membrana tympani becoming tense; while the treading of horses upon stone pavement, the more shrill creaking of carriages, and the rattling of paper may be distinctly heard.

The object of the Eustachian tube is chiefly to allow the free ingress of air into the tympanic cavity in order to provide for the due vibration of the membrana tympani and of the chain of bones. It also, by permitting a free *egress* of air, renders the tympanum a non-reciprocating cavity, and therefore obviates the production of echoes in it, which would materially interfere with perfect hearing. The importance of the Eustachian tube to the integrity of hearing is well known to all practical men by the deafness which always accompanies chronic or acute disease of the tonsils, or occlusion of the canal of that tube from any other cause.

The idea of Boerhaave, and of Bressa, that sounds from without which enter the mouth, or the sounds of one's own voice, were conducted by the Eustachian tube to the labyrinth, is disproved by the simple experiment of holding a sounding tuning-fork or a watch in the open mouth, when it will be always found, if due care be taken to avoid contact, that the sounds proceeding from them are not so well heard as those from without, and the nearer they are brought to the Eustachian tube the less distinctly are they heard. Indeed it may be always noticed that persons deaf from obstruction of the Eustachian tube hear the sounds of their own voices well.

Of the Labyrinth.—The essential part of the organ of hearing is the *vestibule.* This is sufficiently proved by the constancy of this part in the animal series, and by its central position in the most complex ears, so that it is in close relation not only with the other parts of the labyrinth but also with the tympanum.

Sound is conveyed to the labyrinth in a threefold manner: first, by the chain of bones; secondly, by the air in the tympanic cavity; in both these instances the external air is engaged in the conduction; and thirdly, through the bones of the head.

Müller has shown by a very interesting experiment that whilst the air in the tympanum conducts sound to the cochlea through the fenestra rotunda, the chain of bones forms a much better conductor of it to the vestibule through the fenestra ovalis. He imitated the structure of the tympanum by means of a glass cylinder, two inches and one-third in diameter, and six inches long; to the neck of this he fixed a wooden tube, the diameter of whose bore was eight lines. The upper end of this tube was adapted to the mouth of the metal flute-pipe of an organ, one foot in length; its lower extremity was covered with a tense membrane of pig's-bladder, which represented the membrana tympani, the tube itself corresponding to the meatus externus, and the cavity of the glass cylinder to the tympanum. The lower opening of the glass cylinder was closed by a thick piece of cork, in which two holes were cut equidistant from the walls of the cylinder. In these holes, which represented the fenestræ, two wooden tubes were fitted, whose outer openings were covered with membrane. From the membrane of the upper tube to one of these membranes, a rod was extended to imitate the chain of tympanic bones extending between the membrane.

The lower extremity of this apparatus (that namely which was fitted with cork) was now introduced into water, to imitate the connexion between the tympanum and the labyrinth in which sound is conducted from air to liquid. Müller, having plugged his ears,

could by means of a sounding-rod applied in succession to the membrane of each of the artificial fenestræ ascertain the relative intensity of the sonorous vibrations communicated to the water through the two openings, while another person sounded the pipe. He states that the difference was very striking. The sound transmitted by the wooden rod to the opening which represented the fenestra ovalis was in a remarkable degree louder than that propagated through the air of the cavity to the membrane of the other opening.

The results of this experiment lead to the conclusion (which other circumstances confirm), that the vestibule is adapted to receive sounds from the tympanic membrane and external ear, while the cochlea is not easily affected in this manner, but rather, as its structure and connexions point out, that it is fitted to receive vibrations through the bones of the head.

The direct continuity of the walls and the septum (*lamina spiralis*) of the cochlear canal, with the petrous bone, and the minute subdivision of the nerve in distinct canals in the osseous substance, render that portion of the labyrinth most readily affected by the vibrations excited in the cranial bones. The cochlea may therefore be properly considered as that part of the labyrinth which is more immediately affected by sounds communicated through the bones of the head, as the vestibule is the part primarily affected by the sounds communicated through the external ear.

It may be easily shown by some experiments with the tuning-fork, not only that the cranial bones do conduct, but also that sounds inaudible, or imperfectly audible, through the meatus externus may be distinctly heard when the sounding body is brought into contact with a bone of the cranium or face. When the tuning-fork is thrown into vibration by striking it against any solid body, if held near the external ear its vibrations are distinctly heard, but let the stem be applied to the teeth, or to the upper jaw, or to the parietal bone, and the sound appears much louder; or if the fork be held near the ear until the sound has almost died away, and then its stem be applied to the superior maxilla, or to the teeth, the sound seems to revive, and continues for a considerable period while the stem is kept in contact with the bone.

The form of the cochlea probably has reference to the convenient package within the smallest compass of the great number of nerve-fibres which proceed to it.

The remarkable subdivision which the cochlear nerve undergoes, admirably adapts it for the reception of vibrations communicated through the cranial bones. "The spiral lamina of the cochlea," says

Müller, "must be regarded as a surface upon which all the fibres of the cochlear nerve are spread out, so as to be nearly simultaneously exposed to the impulse of the sonorous undulation, and simultaneously thrown into the maximum state of condensation, and again into the maximum state of rarefaction." "This spreading out of the nerve fibres upon the lamina spiralis, insures a more complete participation of the fibres in the impulses communicated by the solid parts of the cochlea." Moreover, "the intensity with which sonorous undulations are communicated to a body, is proportionate to the extent of surface over which they can act on it. Thus, when a sound is excited in water, and is conducted to the stopped ear by means of a rod, the intensity of the sound heard increases with the depth to which the rod is immersed in the water, or with the extent in which it is in contact with the surface of the water."*

The fluid in the scalæ of the cochlea, with the helicotrema or orifice of communication must facilitate the vibrations of the lamina spiralis, and we have already assigned to the cochlearis muscle a protective use to the cochlear nerves.

The Otoliths.—The earthy particles, which, either as pulverulent masses, or as hard porcelainous stones, are connected with the nerves of the membranous labyrinth, must reinforce the sonorous undulations, and communicate to the membranous labyrinth and its nerves vibratory impulses of greater intensity than the perilymph alone could impart. In illustration of this, Müller mentions that sonorous undulations in water are not perceived by the hand itself immersed in the water, but are felt distinctly through the medium of a rod held in the hand. The experiment of Camper is also illustrative. Fill a bladder with water and place a stone or some other hard body in it. The slightest impulse communicated to the bladder disturbs the stone, which consequently produces a greater impression on the hand by which the bladder is supported.

The Semicircular Canals.— There is nothing known of the function of the semicircular canals. Yet their almost constant existence, and nearly constant number evince their physiological importance. In most cases of congenital deafness they are found defective.

Their constancy in the higher animals of number, and of position, which is such that they correspond to the three dimensions of a cube, its length, breadth, and depth, suggested to Autenrieth and Kerner the opinion that they are the parts concerned in conveying a know-

* Müller's Physiology, by Baly, vol. ii. p. 1294. Dr. Young regarded the cochlea, as a micrometer of sound.

ledge of the direction of sounds, a view which is also advocated by Wheatstone. The latter philosopher conceives that we distinguish best the direction of those sounds which are sufficiently intense to affect the bones of the head, and that it is from the vibrations which are transmitted through these bones that our perception of the direction is obtained. The three canals being situate in planes at right angles with each other are affected by the sounds transmitted through the bones of the head with different degrees of intensity, according to the direction in which the sound is transmitted: for instance, if the sound be transmitted in the plane of any one canal, the nervous matter in that canal will be more strongly acted on than that in either of the other two; or if it be transmitted in the plane intermediate between the planes of this canal and the adjacent one, the relative intensity with which those two canals will be affected will depend upon the direction of the intermediate plane. The direction suggested to the mind will correspond with the position of the canal upon which the strongest impression has been made.

There are remarkable differences in the range of the sense of hearing in different individuals, analogous to the differences in the power of vision with regard to colours. Some persons are insensible to certain sounds, which are familiar to other ears, as some are unable to see particular colours. The limits of audition in different individuals may partly depend on the condition of the auditory nerve, and partly upon the size of the membrana tympani. It is probable that animals with very large membranæ tympani can hear much graver sounds than man. The artificial tension of the membrana tympani alluded to at a former page is capable of inducing insensibility to sounds of a grave character, as Dr. Wollaston has shown. The ordinary range of human hearing comprised between the lowest notes of the organ, and the highest known cry of insects, includes, according to Wollaston, more than nine octaves, the whole of which are distinctly perceptible by most ears. Dr. Wollaston has, however, related some cases in which the range was much less, and limited as regards the perception of high notes; in one individual, the sense of hearing terminated at a note four octaves above the middle E of the pianoforte; this note he appeared to hear rather imperfectly, but the F above it was inaudible, although his hearing in other respects was as perfect as that of ordinary ears; another case was that of a lady who could never hear the chirping of the field-cricket; and in a third case, the limit was such that the chirping of the common house-sparrow could not be heard. Dr. Wollaston supposes that inability to hear the piercing squeak of a bat

is not very rare, as he met with several instances of persons not aware of such a sound.

Every one must be conscious that the sensation of sound frequently lasts longer than the exciting cause of it, as the sensation of light does. This has been demonstrated experimentally by Savart, who found in his experiments upon toothed wheels that the removal of one tooth did not produce any interruption of the sound. Other proof of this is obtained from the noise which remains in the ears after long travelling in a coach, or in a train upon a railroad. The subjective phenomena of hearing generally result from some affection of the brain, or of that part of it in which the auditory nerve is implanted. The most common of them are tinnitus aurium, and the buzzing or rushing noise in the ears, which is generally indicative of a deficiency rather than a redundancy of blood in the brain; or it may be caused by some disturbance of local nutrition of the brain giving rise to an irregular developement of nervous power.*

* Upon the subjects discussed in this chapter, the reader may consult the works of Scarpa and Sœmmerring; the excellent article on the organ of Hearing by Mr. Wharton Jones in the Cyclop. of Anat.; Müller's elaborate chapter on Hearing in his Physiology; Dr. Wollaston's paper on Sounds inaudible by certain ears, Phil. Trans. 1820; the article Hearing, Cyclop. Anat.; Dr. Elliotson's Physiology, where the ingenious views of Mr. Wheatstone are briefly stated; and a paper by the latter philosopher in the Journal of the Royal Institution, for July 1827.

CHAPTER XIX.

ENCEPHALIC NERVES EXCLUSIVELY MOTOR IN FUNCTION.—THE THIRD PAIR OF NERVES.—THE FOURTH PAIR.—THE SIXTH PAIR.—THE PORTIO DURA OF THE SEVENTH PAIR.—THE NINTH PAIR.

The nerves which we shall consider in this chapter are purely motor in their function; and, on this account, are conveniently classed together. We shall see, however, that from their occasional anastomosis with sensitive nerves, they contain sentient filaments which serve to inform the mind of the state of the muscles to which their motor filaments are distributed.

The third pair of nerves, or *motores oculorum.* These nerves are connected with the crura cerebri. Each nerve emerges from the corresponding crus, on the side of the locus perforatus posticus, or pons Tarini.

When traced into the substance of the crus, the component fasciculi of each nerve are seen to diverge from each other, and to sink into the dark vesicular matter constituting the *locus niger*. Here, no doubt, the filaments connect themselves with the vesicles of this mass of gray matter.

Each nerve proceeds forwards and outwards, and passes through a canal in that portion of the dura mater which forms the outer wall of the cavernous sinus into the orbit through the spheno-orbital foramen, and just as it has reached this foramen it divides into a superior and an inferior branch, the distribution of which is shewn in the following table.

A. Superior division.	1. *b.* To the levator palpebræ superioris.
	2. *b.* To the superior rectus oculi.
B. Inferior division.	1. *b.* To the internal rectus.
	2. *b.* To the inferior rectus.
	3. *b.* To the inferior oblique.
	4. *b.* To the ophthalmic ganglion, also called the short root of that ganglion.

The anastomoses of the third nerve take place entirely in that stage of its course in which it lies in the outer wall of the cavernous sinus. They are with the ophthalmic division of the fifth nerve, and with the carotid branch from the inferior cervical ganglion of

the sympathetic; and, as has been asserted by a few anatomists, with the sixth nerve.

Function of the third nerve. Proceeding according to the method indicated at page 303, vol. i., we deduce the function of this nerve, from its anatomy in man, from its anatomy in animals, from experiments, and from pathological observation.

From its anatomy in man we judge this nerve to be a motor nerve, for it is distributed entirely to muscles. These muscles are, in addition to the elevator of the upper eyelid, those upon which the principal movements of the eyeball depend, indeed, all the muscles of that organ, except the superior oblique and the external rectus. In addition to these there can be no doubt that the third nerve sends filaments to the muscular apparatus within the eye by the short root of the ophthalmic ganglion, which, after passing through that ganglion, escapes from it under the form of ciliary nerves, which may be traced to the ciliary muscle and to the iris. It is, therefore, the principal motor nerve of the eyeball, regulating all the movements of that organ, excepting those which depend on the external rectus and superior oblique muscles; and it also probably excites the movements of the iris and of the other muscular fibres within the eye. Upon this latter point, however, anatomy speaks less positively, from the fact that other nerves are distributed to the iris besides those derived from the third.

The distribution of the third nerve, in the inferior animals, leads to the same conclusion respecting its function, as that which we have deduced from human anatomy. In all the mammalia it is distributed to the same muscles of the eyeball as in man, and to the iris. In birds a similar arrangement exists, and in some species of this class we observe a remarkable developement of that branch which is distributed to the iris in direct relation with the muscular activity of that structure. In the falcons and eagles, according to Desmoulins, the third nerve is absolutely as large as in man, and this great size is due to the developement of the branch which is distributed to the iris and ciliary muscle.

Experiments on this nerve are difficult of execution, and their results are therefore not free from complication; but such as have been obtained entirely confirm the view of its function which anatomy suggests. These results, as derived from the experiments of Rumbold and Fowler, of Mayo, Valentin, and others, may be summed up as follows:

The application of the galvanic current to the nerve causes a convulsive contraction of the principal muscles of the globe, and of the

iris. The same effect is produced by mechanical irritation of the trunk of the nerve.

Section of the trunk of the third nerve in rabbits or dogs, gives rise to external strabismus, with paralysis of the upper eyelid (ptosis) and dilatation and immobility of the pupil. The eyeball is given up to the influence of the external rectus and of the superior oblique muscles, the former of which being the more powerful determines its permanent position.

The paralysis of the iris, after section of this nerve, is so complete that the most powerful light directed into the eye, is incapable of exciting the least contraction of the pupil. And Mayo's experiments demonstrate that the fifth nerve, which is the only other, except, perhaps, the sympathetic, connected with the iris, does not exert any motor influence upon that membrane.

When the optic nerve is irritated, the third remaining intact and retaining its connexion with the brain, the pupil contracts. This action does not take place if the third nerve have been previously cut. The motor action of the third nerve may, therefore, be excited through the optic nerve. There can be no doubt, indeed, that this is the ordinary method by which contraction of the pupil is produced during life; the stimulus of light falling upon the retina excites the optic nerve and, through it, that portion of the brain in which the third nerve is implanted.

The effects produced by pathological changes affecting the third nerve, or that part of the brain with which it is connected, are in exact accordance with the results derived from experiment.

Paralysis of the levator palpebræ superioris muscle, permanent squinting of the eyeball in the outward direction, and a dilated motionless pupil are the unerring signs of a paralytic lesion affecting the third nerve either at its central extremity or in some part of its course.

The third nerve may, therefore, be stated to be the nerve of motion to the elevator muscle of the upper lid, and a principal nerve of motion to the eyeball, and to the muscular apparatus within the eye. It is a nerve of great importance to vision, not only from its influence over the eyeball itself, but also from its connexion with the muscular structures in the interior, on which the power of adjustment probably depends.

Of the Fourth Pair of Nerves.—These, which were called by Willis "*nervi pathetici*," are the smallest of the encephalic nerves. They are also remarkable for the very long course which they take from their origin to their point of exit from the cranium.

The origin of the fourth nerve may be referred to the mesocephale, from the superior surface of which it emerges in close connexion with the testes, or immediately behind them. Its true origin is doubtless from the olivary columns as they extend upwards beneath the quadrigeminal tubercles.

The fourth nerve emerges from the cranium through a canal in the dura mater, situate near the posterior clinoid process of the sphenoid bone, external to that in which the third nerve is lodged. It passes along the outer wall of the cavernous sinus beneath the third nerve, and in entering the orbit it rises above that nerve, and lies immediately beneath the periosteum, attaching itself to the orbital surface of the superior oblique muscle, into the posterior third of which it penetrates.

This is the only muscle which the fourth nerve supplies, and the nerve appears to be wholly lost in it. But as it passes through its canal in the dura mater, it gives off a branch, which, taking a retrograde course, passes into the tentorium cerebelli as far as the lateral sinus, where it subdivides into two or three filaments.

In its course it forms but few connexions, and those apparently not constant. As it crosses the cavernous sinus it anastomoses with the sympathetic, and, as it enters the orbit, with the lachrymal.

That this nerve is the motor nerve to the superior oblique muscle anatomy does not allow us to doubt, for the muscle receives no other.

Experiments and pathological observation have thrown no satisfactory light upon its function.

In animals of great power of expression, as in apes, according to Sir C. Bell, this nerve, as well as the superior oblique muscle, is large.

Of the Sixth Pair of Nerves.—These nerves emerge from between the fibres of the anterior pyramids immediately behind the posterior margin of the pons Varolii. It is not improbable that the true origin of each nerve is from the central part of the medulla oblongata, *the olivary columns*, and that the nerves pass between the fibres of the pyramids without forming any real connexion with them.

The sixth nerve has a straight, but very short intracranial course; it penetrates the dura mater, and passes over the outside of the carotid artery, between it and the lining membrane of the cavernous sinus, entering the orbit between the two origins of the rectus externus muscle, to the ocular surface of which it is entirely distributed.

As the sixth nerve is passing along the outer side of the internal

carotid artery, it forms a very celebrated anastomosis with the sympathetic, by means of two large and distinct branches, and it sometimes anastomoses with the nasal branch of the fifth.

Anatomy points to the function of this nerve as distinctly as it does to that of the fourth. The sixth nerve can have no other office than that of regulating the movements of the abductor muscle of the eye. Experiment fully confirms this conclusion, and a few cases have been observed in which internal strabismus was found to accompany compression of the nerve by a tumor.

Of the Facial Nerve.—(*Portio dura* of the seventh pair.)—This is one of the most interesting and remarkable of the motor nerves. Its close proximity to the auditory nerve led Willis to class it along with that nerve. The former nerve is soft in its structure, and its bundles loosely coherent; the latter is more compact, and surrounded by a neurilemma of sufficient density to give to it a power of resistance very superior to that of its neighbour.

These two nerves lie in a fossa situate on either side of the medulla oblongata, and behind the posterior edge of the pons, bounded on the outside by a small lobule of the cerebellum, called *the flock* by Reil, or the lobule of the vagus or of the auditory nerve; the floor of this fossa is formed by the restiform column. The portio dura nerve, which lies inside the portio mollis, penetrates the restiform column, and through it may be traced to the central part of the medulla oblongata, *the olivary columns*, where it connects itself with the vesicular matter.

In examining the distribution of the facial nerve, it will be found convenient to divide it into three stages, and to enumerate its branches in each stage.

The first stage is *intracranial*, from its origin to its exit at the internal auditory meatus. In this stage it forms a connexion with the auditory nerve by the *portio intermedia* of Wrisberg, an oblique branch of communication, which seems like a fasciculus of fibres passing off from the portio dura, and accompanying the auditory nerve into the labyrinth. This branch was described by Arnold and Gœdechens as a second root of the facial nerve, but inasmuch as it does not form a connexion with the centre, distinct from that which the principal fibres of the nerve have with it, this view is not tenable. Regarding the facial as a motor nerve, this branch may possibly be viewed, as conveying motor influence to the muscular apparatus of the cochlea, which we have discovered.

The second stage is contained in the *aqueductus Fallopii.* In its passage through this canal a gangliform swelling is formed on

the nerve where it is joined by the Vidian which comes through the hiatus Fallopii, *intumescentia genuformis*. A question arises as to the nature of this swelling; is it a ganglion, or, is it merely the result of the separation of the fibres of the nerve at this situation? We have failed to satisfy ourselves by microscopic examination of the existence of vesicular matter in it, but we have found a large number of gelatinous fibres in it, as well as of tubular fibres.*

At this swelling the facial forms a communication by means of the *greater superficial petrosal nerve* with Meckel's ganglion, and by the *lesser superficial petrosal nerve*, with the otic ganglion; a third branch less constant than these two, is distributed to vessels and dura mater on the surface of the petrous bone. As it lies in the aqueduct of Fallopius, the facial nerve gives off the following branches. 1. A branch to the membrane of the fenestra ovalis. 2. A twig to the stapedius muscle. 3. The chorda tympani. 4. An anastomotic twig with the auricular branch of the vagus nerve.

The third stage commences at the stylomastoid foramen; here the nerve passes obliquely through the parotid gland, in the substance of which it divides into its terminal branches. Immediately on its emergence from the stylomastoid foramen, it gives off. 1. The *posterior auricular*, or *auriculo-occipital*, distributed to the small muscles of the ear, and the occipital muscle. 2. The *stylohyoid* branch to the stylohyoid muscle. 3. The *submastoid* branch to the digastric muscle. And lastly, it divides into two branches, the *cervico-facial*, distributed to the platysma, and to the muscles of the lower lip and chin, and the *temporo-facial*, which is distributed to the orbicular muscle of the eyelids, the corrugator supercilii, and the muscles of the nose and upper lip. The plexiform distribution of these nerves on the face forms the well-known *pes anserinus*. The facial nerve anastomoses freely with the superficial temporal, frontal, infra-orbital, buccal and mental branches of the fifth pair, and with branches of the cervical plexus.

Function of the Facial Nerve.—Referring to the anatomy of this nerve, we find it distributed by the vast majority of its fibres to muscles, and those minute branches, respecting the ultimate destination of which some doubt exists, may be, and probably are, distributed to muscular fibres. The muscles which are supplied by the facial nerve are chiefly those upon which the aspect of the countenance and the balance of the features depends. The power of closing the

* Morganti has lately published an elaborate paper, in which he maintains the ganglionic character of this swelling.—Annali Univ. di Medicina, 1845.

eyelids depends on this nerve, as it alone supplies the orbicularis palpebrarum; and likewise that of frowning, from its influence upon the corrugator supercilii. Anatomy indicates, therefore, that this nerve is the motor nerve of the superficial muscles of the face and ear, and of the deep-seated muscular fibres within the ear.

This conclusion is abundantly confirmed by comparative anatomy. For wherever the superficial muscles of the face are well developed, and the play of the features is active, this nerve is large. In monkeys it is especially so. That extremely mobile instrument, the elephant's trunk, is provided with a large branch of the facial as its motor nerve. In birds, on the other hand, it is very small, being limited to the stylohyoid branch.

Section of the nerve, at its emergence from the stylomastoid foramen, has been followed by paralysis of the muscles of the face, and of the orbicularis palpebrarum, in the hands of all experimenters. Formerly when this nerve was supposed to preside over the sensibility of the face, it was thought to be the seat of tic douloureux, and was upon several occasions cut. But this operation yielded no relief to the sufferings of the patient, and only served to illustrate the function of the nerve, since it was always succeeded by paralysis of the face on that side, total loss of control over the features, of the power of frowning, and of closing the eyelids.

The diseased states of the facial nerve illustrate its physiology in the most interesting manner. It may be paralysed from the influence of cold, benumbing its superficial fibres, or from the compression of a tumour at the angle of the jaw, or from a carious state of the petrous portion of the temporal bone. From whatever cause the paralytic state arises, the effect is invariably the same; the patient is unable to close his eyelids, and in some rare cases he has not the power even of approximating them to each other in the least degree. He cannot move the ala nasi or either lip on the affected side, and if told to purse up the mouth, as in whistling, he is unable to do it. When he laughs, the movement is all on one side, and the angle of the mouth on the sound side is drawn upwards towards the ear, whilst that on the paralysed side hangs below its ordinary level. With so much paralysis of the superficial muscles, the deeper seated ones which direct the masticatory movements of the lower jaw, and are supplied by the fifth nerve, remain unaffected, and the sensibility of the face is unimpaired.

When the paralytic affection of this nerve has been of long standing there is great wasting of the muscles on that side of the face, and even the buccinator, which is supplied by the fifth nerve also,

suffers to such an extent that it becomes reduced to a mere inert membrane, and flaps to and fro as the patient speaks, interfering to a great degree with the clearness of his articulation.

That the facial nerve in some degree influences the movements of the soft palate, has been suggested by the record of cases in which palsy of the muscles on one side of the face has been accompanied by paralysis of the corresponding half of the velum. That this symptom sometimes accompanies the other signs of this form of palsy, cannot be doubted; but the frequency of its absence is sufficient to denote the trifling influence of the nerve upon the palatine muscles. Valentin irritated the greater superficial petrosal nerve, which is the probable source of any nervous filaments from the facial to the muscles of the palate, but failed to excite any movement of those muscles in fifteen experiments.

Much uncertainty exists likewise as regards the function of the chorda tympani. Regarding it, as we do, as a branch of the portio dura, we think it must exercise a motor influence upon the parts to which it is distributed, of which the principal is the duct of the submaxillary gland. But the curious relation which it bears to the malleus and incus denotes that it may have something to do with the mechanism of the organ of hearing.

It has been made a question how far the facial nerve possesses any sensibility, and from whence it derives sensitive fibres. That irritation of it causes pain, has been sufficiently proved by various experimenters, and it appears that the sensibility is more marked after the nerve has passed through the parotid gland. The sources of the sensitive fibres appear to be clearly indicated by the various anastomoses which the facial nerve forms in its several stages—in the Fallopian aqueduct with the vagus nerve, in the face with the fifth nerve, and in the neck with spinal nerves; the communications with the fifth nerve being very numerous. There are therefore sufficient means of communication with sensitive nerves to explain the sensibility of the facial without its being necessary to have recourse to the theory of Arnold, and to rank it with the double-rooted nerves.

Of the Ninth or Hypoglossal Nerve.—The origin of this nerve is from the side of the medulla oblongata along the anterior margin of the olivary body. Ten or twelve fasciculi of fibres emerge here from the central part of the medulla oblongata, and unite into two bundles, which coalesce and emerge as one nerve through the anterior condyloid foramen.

The ninth nerve, on escaping from the anterior condyloid foramen, passes outwards, and winds forwards around the pharynx, to

the deep surface of the tongue, being closely related to the internal carotid artery and the jugular vein, and winding round the external carotid, in its course to the upper and anterior part of the neck.

Immediately after its emergence it forms anastomoses with the vagus nerve, the superior cervical ganglion, and with the cervical plexus, and then it gives off, 1. The descending branch, which forms remarkable anastomotic arches with branches of the second and third cervical nerves, either within or in front of the sheath of the common carotid artery and jugular vein. From the convexity of this arch or these arches, there pass branches to the sterno-hyoid, and sterno-thyroid muscles and to the anterior belly of the omo-hyoid. 2. It gives nerves to the thyro-hyoid, genio-hyoid, hyo-glossus, and styloglossus muscles. 3. On the inferior surface of the tongue it breaks up into its terminal, or glossal branches which pass into the muscular structure of the tongue.

As the hypoglossal nerve crosses the hyoglossus muscle it forms an anastomosis with the lingual branch of the fifth pair.

Function of the Ninth Nerve.—As this nerve has no other connexion than with muscles we cannot regard it in any other light than as a motor nerve. The muscles to which it is distributed are those of the tongue, and as this is the principal nerve to these muscles, we may justly regard it as the motor nerve of the tongue. The other nerves of the tongue, the lingual branch of the fifth and the glosso-pharyngeal, are obviously traceable to the mucous membrane.

In the lower mammalia the ninth nerve is distributed precisely as in man, and it is proportional in size to the muscular activity of the tongue.

Numerous experiments have been made on this nerve. Section of it on one side paralyses the motor power of the tongue on that side. And galvanic irritation of it throws the muscles on the same side into convulsive action.

Several instances have been observed of tumours compressing this nerve, and causing paralysis of the muscles of the tongue on the same side. The tongue participates in the hemiplegic paralysis which results from an apoplectic clot in the brain, or other extensive disease of that organ, along with all those parts whose nerves are implanted in some part of the extended centre of volition, and are ordinarily excited by a mental stimulus. In such cases the loss of power in the tongue is usually indicated by its deviation to the paralysed side in its protrusion, though occasionally the tip is turned towards the sound side.

We may then conclude from human and comparative anatomy, from experiment and pathological states, that the ninth nerve is the motor nerve of the tongue. Its anastomoses with the vagus, and with the fifth, make it probable that it contains some sensitive filaments, and this is confirmed by experiments which shew that some sensibility is possessed by the nerve, and that this is greatest the nearer we approach the tongue. But that it has no influence upon taste or upon the common sensibility of the organ, is proved by the unimpaired state of both those powers, after complete section of the nerve.*

* In addition to the principal systematic works on physiology, reference may be made to Valentin, de Functionibus Nerv. Cerebr.; the Papers of Sir C. Bell, collected in an octavo volume, 1844; Mayo's papers in his Anat. and Physiol. Commentaries, and his Physiology; Longet sur le Système nerveux.

CHAPTER XX.

OF THE COMPOUND ENCEPHALIC NERVES. THE FIFTH PAIR. THE EIGHTH PAIR.

It is proposed to devote this chapter to the examination of the physiological history of those encephalic nerves which, from their compound nature, combine the functions of sensitive and motor nerves. These are the fifth pair and the eighth pair.

The fifth pair of nerves is one of the most interesting and extensively connected nerves in the body. It presents a remarkable resemblance to spinal nerves in its mode of origin, a fact which bears strongly on the determination of its functions. The first point of resemblance is that its origin is by two roots, one large, and the other small; and secondly, its larger root is involved in a ganglion, the two roots being quite distinct until after the formation of the ganglion, when the lesser one coalesces with one of the nerves which springs from the ganglion, to form the inferior maxillary nerve.

The two roots are implanted in the same column of the medulla oblongata. They remain, however, quite distinct in the substance of the medulla. Penetrating the latter at the crus cerebelli, between the transverse fibres of the pons, each root may be traced through a separate but nearly parallel course downwards to the olivary column, where each forms its separate connexion with the vesicular matter.

The ganglion (*ganglion Gasserii*) which is formed upon the larger root of the fifth nerve is situate in the middle fossa of the cranium upon the upper surface of the petrous bone, and the middle lacerated foramen, and behind the great ala of the sphenoid. It is of a triangular form, its base curvilinear and directed forwards and outwards. From this base there proceed three nerves, the ophthalmic on the inside, the superior maxillary in the middle, and the inferior maxillary on the outside. Of these the first two consist exclusively of fibres derived from the larger root and ganglion; the third, the inferior maxillary, is composed of fibres derived from both roots. This, therefore, is the only portion of the fifth nerve which is strictly compound, and it constitutes the largest portion of the nerve.

The distribution of the nerve may be understood by reference

to the subjoined tabular arrangement of the distribution of each of its three divisions.

TABULAR VIEW OF THE DISTRIBUTION OF THE FIFTH NERVE.

I. OPHTHALMIC—(anastomoses with sympathetic).

a. Lachrymal
- 1. *b.* To lachrymal gland.
- 2. *b.* To unite with temporo-malar branch of supra-maxillary nerve.
- 3. *b.* To external canthus, eyelids, &c.

b. Frontal .
- 1. Supra-trochleator *b*, to integuments of internal canthus, conjunctiva, lids, &c.
- 2. Continued frontal nerve, or supra-orbital.

c. Nasal .
- 1. Lenticular *b*, to the ophthalmic ganglion.
- 2. Ciliary nerves,—two in number.
- 3. Nasal *b*, to the mucous membrane and skin of the anterior part of the nostril.
- 4. Infra-trochleator, to the inner canthus and side of the nose.

II. SUPERIOR MAXILLARY—(three stages, cranial, spheno-maxillary, orbital).

a. Temporo-malar *b.*—Anastomoses with the lachrymal and is distributed to the integument of the temporal and malar region.

b. Spheno-palatine *b.*—Two or three in number, which pass to the spheno-palatine ganglion.

c. Post. superior dental *b.*—Two or three in number, going to the posterior teeth of the upper jaw; one branch passing along the interior of the antrum, and anastomosing with the anterior superior dental.

d. Ant. superior dental *b.*—Supplies the anterior teeth of the upper jaw.

e. Facial . . .
- 1. Palpebral.
- 2. Labial.
- 3. Nasal.

Supplying the integuments of those regions.

III. INFERIOR MAXILLARY.

a. Masseteric *b.*—To the masseter muscle.

b. Deep temporal *b.*—Two in number, to the temporal muscle.

c. Buccal *b.*—Anastomoses with branches of the facial, and goes to the external pterygoid and buccinator muscles, and to the mucous membrane of the mouth.

d. Pterygoid *b.*—To the circumflexus palati and internal pterygoid muscle.

e. Superficial temporal *b.*—Anastomoses with the facial, and is distributed to the skin of the temporal region and external ear.

f. Inferior dental *b.*
- By its mylohyoid branch to the mylohyoid and digastric muscles.
- To the teeth, alveoli and gums of the lower jaw; and by the mental branch to the integuments and mucous membrane of the lower lip.

g. Lingual *b.* .
- Is joined by the chorda tympani.
- Connecting filaments to the submaxillary ganglion or plexus.
- Anastomotic branches to the ninth nerve.
- Branches to mucous membrane of the tongue.

Function of the fifth nerve.—The determination of the functions of the roots of spinal nerves has afforded the clue to that of the functions of the roots of the fifth nerve. The analogy of the smaller root of the fifth with the anterior spinal root, and of the larger one with the posterior spinal root has long been admitted by anatomists. Hence an analogy of function must be admitted, and the former must be viewed as consisting of motor fibres, the latter of sensitive ones; and by tracing each of the three great divisions of the nerve, we may determine its function by its constitution, according as it derives its fibres from either root or from both. The ophthalmic and superior maxillary are composed of fibres derived exclusively from the larger root; they are, therefore, sensitive nerves. The inferior maxillary consists of fibres derived from both roots, and consequently is both motor and sensitive. Sir C. Bell, in his original exposition of the functions of this nerve, fell into error from having neglected to avail himself of this method of analysing the constitution of each of its three divisions, from which he would have seen that it is the inferior maxillary alone which derives its fibres from both roots, and which perfectly resembles a spinal nerve in constitution.

The distribution of the three divisions of the fifth nerve confirms most amply the view of its physiology suggested by the anatomy of its origin. The ophthalmic and superior maxillary are distributed entirely to sentient surfaces, or anastomose with motor nerves (the facial). They supply the skin of the forehead, of the eyelids, the conjunctiva, the eyeball, the mucous membrane of the nostrils, the integuments of the face, the upper lip, the nose, the beard on the upper lip, the integument of the ear, the temple, and the whiskers; they are the sensitive nerves to these regions. The inferior maxillary has two distinct sets of branches, the one by which the muscles of mastication are supplied—the other, which go to the integuments of the lower lip and chin, and the beard, and the mucous membrane of the mouth and tongue. This nerve is, therefore, the nerve of mastication, and of sensation to the surfaces above-named.

Repeated experiments in the hands of various physiologists, none of which, however, were more conclusive than those of Mayo, indicate the same views of function. Division of the ophthalmic or of the superior maxillary induced loss of sensibility without muscular paralysis, leaving only such an impairment of the motor power as destruction of the sensitive nerves invariably produces, by impairing the power of exact adjustment, for which a high degree of sensibility is necessary. But when the inferior maxillary nerve was cut, then

both the power of mastication was destroyed on the same side, and the sensibility of the lower part of the face and tongue was lost. If the nerve were divided in the cranium, the whole side of the face and forehead, with the eyeball and nose, became insensible, and the muscles of mastication were paralysed. Irritants might then be applied to the eyeball, without exciting winking, or causing pain, and strong stimulants might be introduced into the nostrils without creating the least irritation. When the trunk of the nerve within the cranium of an ass was irritated, the jaws closed with a snap from the excitation of the motor fibres, which are distributed to the muscles of mastication.

The conclusions which we draw from anatomy and from experiment are confirmed by the histories of cases in which the fifth nerve had been diseased. In such instances we may observe the most marked separation of the motor and sensitive power, when the larger portion only or the two superior divisions of the nerve are affected, and we find both motion and sensation destroyed when the whole trunk of the nerve is involved in the disease. It is not uncommon in such cases to find the eyeball totally insensible to every kind of stimulus, the nose quite unexcitable by the fumes of ammonia, or the most pungent vapours, and the mucous membrane of the mouth so insensible to the contact of foreign matters that a morsel of food will sometimes remain between the gum and the cheek until it has become decomposed. The insensibility of the eyeball exposes it to the permanent contact of irritating particles of dust, &c., which excite destructive inflammation of its textures. The whiskers may be pulled forcibly without sensation. The muscles of mastication become wasted and inert, as shown by the distinct depression in the regions of the masseter and temporal muscles, but the superficial muscles, on which the play of the features depends, preserve their natural condition.

The fifth nerve may, therefore, be regarded as the motor nerve in mastication, and the sensitive nerve to that great surface, both internal and external, which belongs to the face and anterior part of the cranium. From its great size, and the large portion of the medulla oblongata with which it is connected, it may excite other nerves which are implanted in that centre near to it. Thus it may be an excitor to the portio dura, as in winking—or to the respiratory nerves, as in dashing cold water in the face, or in sneezing. Its lingual portion distributed to the mucous membrane of the tongue is at once a nerve of taste, touch, and common sensibility, and its connexion with the papillary structure of the red parts

of the lips constitutes it a pre-eminently sensitive nerve of touch in those regions.

The study of the pathological conditions of this nerve illustrates its physiology in a highly interesting manner. In the dentition of children, whether primary or secondary, it is always affected, more or less: and in excitable states of the nervous centres, the irritation of it consequent upon the pressure of the teeth often gives rise to convulsions, the brain and spinal cord being irritated; and we can often trace to such irritation, whether in infancy or in childhood, the foundation of epileptic seizures in subsequent years. Painful affections of the face (*neuralgia*) have their seat in this nerve; *tic-douloureux* for example. Many of the instances of painful affection of this nerve or of branches of it, which come under our observation, are well marked examples of reflected sensation, the primary irritation being conveyed to the centre by the vagus or the sympathetic from the stomach or intestinal canal. No one of these is so common as the pain over the brow, which so often follows derangement of stomach digestion; and which may frequently be instantaneously removed by taking away the source of irritation, as by neutralizing free acid in the stomach. Frequently also the branches of this nerve, in greater or less number, on one or both sides, may according to the humoral view, form a focus of attraction for a morbific matter generated in the blood, in persons exposed to the paludal poison, or in persons of rheumatic or gouty constitution; in these cases, as in most others of similar pathology, the neuralgia occurs in paroxysms of greater or less severity, each paroxysm being followed by a period of convalescence, which lasts, it may be supposed, until the morbid matter has been again accumulated in quantity sufficient to induce a high degree of irritation of the nerves.

Of the Eighth Pair of Nerves.—We must examine separately the anatomy and physiology of each of the three nerves which taken together constitute the eighth pair, and first,

Of the Glossopharyngeal.—This nerve consists of several small fascicles of fibres, which lie close together, and are implanted in the upper part of the medulla oblongata behind the olivary body. The fibres penetrate to the centre of the medulla (the olivary columns) where they connect themselves with a special accumulation of vesicular matter.

The glossopharyngeal nerve escapes through a small foramen in the dura mater, at the anterior part of the foramen lacerum posterius. Immediately after it has passed this foramen, a small ganglion which involves only some of the fibres of the nerve, is formed

upon it. This is the *ganglion jugulare*, discovered by Ehrenritter. Beyond this, and lodged in a fossa in the side of the jugular foramen, is another ganglion which involves all the fibres of the nerve; this is the *ganglion petrosum*, originally described by Andersch. After its escape through the jugular foramen, the glossopharyngeal descends by the side of the pharynx, between the styloglossus and stylopharyngeus muscles, and in the region of the tonsil breaks up into its terminal branches.

From the ganglion of Andersch, a nerve passes off, and enters the cavity of the tympanum, occupying a groove upon the surface of the promontory beneath the lining membrane of the tympanum. This branch, lately called the branch of Jacobson, although described by Andersch and Winslow, divides into six filaments, which form the *tympanic plexus* or anastomosis. These filaments are as follow:—1. To the membrane of the fenestra ovalis. 2. To that of the fenestra rotunda. 3. To the carotid plexus in the carotid canal. 4. To the mucous membrane of the Eustachian tube. 5. An anastomotic branch, which passing through the upper wall of the tympanum unites with the greater superficial petrosal nerve. 6. An anastomotic branch to the otic ganglion, called by Arnold the *lesser superficial petrosal nerve.*

Near the petrosal ganglion the glossopharyngeal nerve forms anastomoses with the facial and the par vagum.

The following are the terminal branches of the glossopharyngeal nerve. 1. A branch to the digastric and stylopharyngeal muscles. 2. Three or four carotid filaments which descend along the internal carotid artery, and may be traced as far as the bifurcation of the common carotid. These nerves anastomose with others from the superior cervical ganglion, and form a plexus round the carotid artery. 3. Tonsillitic branches, which are numerous, and along with nerves from the vagus and from the superior cervical ganglion of the sympathetic, form a plexus beneath the mucous membrane in the vicinity of the tonsil, which is called the *pharyngeal* or *tonsillitic* plexus. Some of the branches of this plexus are distinctly connected with the mucous membrane, others with the muscular fibres of the pharynx. 4. Pharyngeal branches, which are distributed to the mucous membrane of the wall of the pharynx. 5. Lingual branches; these are given to the mucous membrane at the base and side of the tongue, and one may usually be traced into the soft palate.

From the preceding statement it appears that the distribution of the glossopharyngeal nerve is chiefly, if not exclusively, to sentient surfaces. Even its tympanic branch is connected with the lining

membrane of that cavity and of the Eustachian tube. But its principal branches are those on the pharynx and tongue, which latter region, however, it must not be forgotten, has another nerve distributed to its mucous membrane. Its digastric branch seems to be anastomotic with a similar one from the facial.

The mode of origin of this nerve affords but a feeble clue to the discovery of its physiological import. Müller and others attach some value to the existence of the ganglion, involving only some of its fibres shortly after their origin, and from the analogy with spinal nerves and with the fifth, they infer that the glossopharyngeal must be a compound nerve of double origin, containing both motor and sensitive fibres. There is not, however, sufficiently certain evidence of the existence of two roots to this nerve to justify us in founding upon it an argument respecting its function.

The most extensive series of experiments on this subject are those of Dr. John Reid, and they have very satisfactorily developed the proper functions of the nerve.

Section of the nerve, or irritation of it, always caused pain, and hence it may be said to contain fibres of common sensation.

When the trunk of the nerve was irritated before giving off its pharyngeal branches, extensive muscular movements of the throat and lower part of the face were produced. It was found that these movements were equally produced, and to as great an extent, if the nerve had been cut a short way below its exit from the cranium, and the cranial end of it irritated. Hence it was evident that the movements were caused, not by the direct influence of the branches of the glossopharyngeal upon the muscles, but by that of the cranial end of the nerve upon the medulla oblongata, whence the change was propagated to the muscles through the fibres of the vagus nerve and through those of the facial, which emanate from the same part of the nervous centre.

This view of the mode in which the glossopharyngeal causes muscular action is confirmed by the result of experiments on it in animals just dead. When the nerve was irritated under those circumstances, no movements could be excited, provided it was sufficiently insulated from the pharyngeal branches of the vagus. Now, were the fibres of the glossopharyngeal motor, there is no doubt that mechanical irritation of them would have caused muscular contraction.

Hence, the glossopharyngeal is one of those sensitive nerves which is capable of exciting motion through its influence upon motor fibres implanted immediately contiguous to it in the nervous centre.

It appeared, however, that other fibres were capable of exciting the

movements of the pharynx, for when the trunk of the nerve was cut on both sides, the movements of deglutition continued.

Dr. Reid's experiments showed that section of the lingual branches of this nerve did not destroy the power of taste, and therefore that the glossopharyngeal cannot be regarded, according to the views of Panizza, as the sole nerve of that sense. And this accords so completely with anatomy, which shows that a part of the tongue, enjoying the gustatory power, is supplied by the fifth nerve and that only, and that another part, also enjoying the same power, is supplied only by the glossopharyngeal, that no doubt can be entertained of the correctness of the view which assigns gustatory power to this nerve as well as to certain filaments of the fifth pair. At a former page we have referred to a case of paralysis of the fifth nerve in which, while taste was altogether lost in the anterior part of the tongue, it continued at its posterior part; the fifth nerve which supplies the tongue in the former situation being paralysed, whilst the glosso-pharyngeal, distributed in the latter region, was free from disease. Two very interesting cases confirmatory of the same view have since been published by Mr. Dixon, in the Med. Chir. Trans. vol. xxviii.

Disease, limited to this nerve, is of extremely rare occurrence. In one instance that we have met with, in which its neurilemma was considerably thickened, there was not only total inability to swallow, but likewise the mucous membrane of the pharynx was quite insensible to stimuli, and that surface of the fauces, which, in health, may be excited by the slightest touch of a feather, admitted even of friction without any uneasiness to the patient, or the least muscular contraction.

The functions of the glossopharyngeal nerve are highly worthy of an attentive study, in reference to the very important question discussed at a former page, as to the existence of distinct spinal and cerebral fibres. We have in it an example of a nerve at once excitor and sensitive; it is a most marked instance of a nerve, not motor in itself, but capable of exciting motion by its influence on others. Yet no part of the surface to which it is distributed can be touched without sensation being excited, and with it motion. The stimulation even of that portion of the tongue which receives filaments from it is capable of exciting the pharyngeal muscles to contract, although the action is not so energetic as when the stimulus is applied to the isthmus faucium. In examining the fauces of patients, the practitioner has frequent opportunity of observing the extraordinary sensibility of the mucous membrane, where the glossopharyngeal nerve

ramifies, and the remarkable rapidity with which the pharyngeal muscles respond to the slightest stimulus applied to it.

The following conclusions may be adopted respecting the glossopharyngeal nerve.

1. It is the sensitive nerve of the mucous membrane of the fauces and of the root of the tongue, and in the latter situation it ministers to taste and touch as well as to common sensibility; and being the sensitive nerve of the fauces, it is probably concerned in the feeling of nausea which may be so readily excited by stimulating the mucous membrane of this region.

2. Such are its peripheral organization and central connexions, that stimulation of any part of the mucous membrane in which it ramifies, excites instantly to contraction all the faucial muscles supplied by the vagus and the facial nerves, and the permanent irritation of its peripheral ramifications, as in cases of sore throat, will affect other muscles supplied by the facial nerve likewise. It is, therefore, an excitor of the movements necessary to pharyngeal deglutition.

Of the Vagus Nerve. The *par vagum* or *pneumogastric nerve*, is of all the encephalic nerves the most extensively connected.

This nerve emerges from the medulla oblongata immediately below the glossopharyngeal, by from eight to ten fasciculi of fibres which pass outwards to an opening in the dura mater, through which it escapes in company with the spinal accessory. The line along which its fascicles emerge from the medulla is placed a little behind the posterior edge of the olivary body. These fascicles penetrate the olivary columns, and are there implanted in a special accumulation of vesicular matter.

A ganglion is formed upon the vagus nerve immediately it enters the canal of the dura mater. From this ganglion some small nerves come off. Shortly after the emergence of the vagus nerve from the base of the skull, another gangliform enlargement is formed upon it, which Arnold calls, *plexus gangliformis.* It is at the situation of this enlargement that the union between this nerve and the internal branch of the spinal accessory takes place.

At its upper part the vagus forms numerous anastomoses, at first by nerves given off from the ganglion. These are, *a*, with the ganglion petrosum of the glossopharyngeal, *b*, with the carotid branch of the superior cervical ganglion, *c*, with the facial nerve, through the branch called by Arnold *the auricular*, which is situate in the jugular fossa outside the vein, and is seen through its coats when that vessel is laid open. It anastomoses likewise with the ninth

nerve, with the cervical plexus, and with the superior cervical ganglion, in a manner sometimes very intimate.

The following branches are given off by the vagus nerve.

1. *The Pharyngeal Branch.*—This is believed by some anatomists to be derived altogether from the spinal accessory nerve, through its anastomosis with the vagus. It forms, along with the glosso-pharyngeal, some cervical nerves, and sympathetic filaments, the pharyngeal plexus, and its branches seem to be distributed to the muscles of the pharynx. Sometimes there are two pharyngeal branches, a superior and inferior.

2. *The Superior Laryngeal Nerve*, which gives off the external laryngeal nerve to the crico-thyroid muscle, and is itself distributed to the mucous membrane of the larynx, and sends an anastomotic branch to the inferior laryngeal nerve.

3. *Cervical Cardiac Branches.*—These are at least two in number on each side, and they pass down in front of the innominata on the right and of the aortic arch on the left, and contribute to form the small plexus between the aorta and pulmonary artery.

4. *The Inferior Laryngeal Nerve.*—This important nerve is distributed to all the intrinsic muscles of the larynx, except the crico-thyroid. The peculiarity of its course has given it the name *recurrent.* It has interesting relations differing on the right and left side. Arising on the left side just in front of the arch of the aorta, it winds round the concavity of that vessel, and ascends between the œsophagus and the trachea to the lower edge of the inferior constrictor of the pharynx. The nerve of the right side separates from the trunk just above the subclavian artery, and winds round it, ascending in the neck to a similar destination.

Both recurrent nerves before their ultimate distribution give off filaments to the heart, to the trachea, to the œsophagus, and to the inferior constrictor of the pharynx.

5. *Inferior or Thoracic Cardiac Branches*, distributed to the pericardium, and the cardiac plexus.

6. *Anterior Pulmonary Branches*, passing in front of the bronchial tube at the root of the lung, and penetrating the pulmonary substance, along with the ramifications of the bronchus, and of the pulmonary artery.

7. *Œsophageal Branches*, which are very numerous, and distributed to the œsophagus, throughout its entire length.

8. *Tracheal Branches*, to the mucous membrane and muscular fibres of the trachea.

9. *Posterior Pulmonary Branches;* these go to form the posterior

pulmonary plexus, of which there are a right and a left plexus, which anastomose freely with each other, situate behind the bifurcation of the trachea. The ramifications of this plexus follow chiefly the course of the bronchial tubes, being distributed to their mucous membrane and muscular fibres.

After giving off the pulmonary branches, the vagi nerves pass down along the œsophagus, giving off branches to it, and passing through the œsophageal opening of the diaphgram are distributed to the stomach. The *left* nerve passes in front of the cardiac orifice, sends some filaments over the splenic *cul de sac*, and follows the course of the lesser curvature; some of its branches passing in the lesser omentum to the liver, whilst the rest are distributed to the coats of the stomach. The *right* nerve passes behind the cardiac orifice, and after giving several branches to the stomach, sinks into the solar plexus.

This outline of the anatomical distribution of this extensively connected nerve is sufficient to show that it is devoted to muscular fibres as well as to sentient surfaces, and that it must be regarded as a compound nerve, sensitive as well as motor. The existence of the ganglion, which involves all the fibres of the vagus nerve, in the canal of the dura mater, has led to the opinion that all its proper fibres are sensitive, while those branches which go to muscles are derived from its large anastomosis with the spinal accessory. Whether this view be correct or not, it is certain that a free communication exists just below the basis cranii between the vagus and the spinal accessory nerves.

The branches of this nerve, which anatomy shows to be purely motor, are the pharyngeal, and the inferior laryngeal, whilst the cardiac, œsophageal, pulmonary, and gastric branches are doubtless of a mixed character, and the superior laryngeal is purely sensitive, with the exception of those of its fibres which form the external laryngeal nerve.

The distribution of the vagus nerve in the inferior mammalia corresponds very closely with that in man, and so far confirms the views of function suggested by human anatomy. Its connexion with the sympathetic in some of the mammalia (the dog and cat for instance) is more intimate than in man, for the upper part of the cervical portion of the sympathetic is closely connected with it, so that they appear to form but one nervous trunk. The general disposition of the nerve in birds and reptiles does not materially differ from that in man, and it has an analogous arrangement in fishes.

The results of the numerous experiments of which this nerve has

been made the subject, accord in a striking manner with the conclusions deducible from anatomy. Thus, mechanical and galvanic irritation of the pharyngeal branches has always produced contractions of the pharynx: irritation of the superior laryngeal nerve causes contraction of the crico-thyroid muscle only, whilst that of the inferior laryngeal causes forcible contraction of the laryngeal muscles as well as of the inferior constrictor of the pharynx. In a living animal the slightest touch to the mucous membrane of the glottis will cause the instant closure of that fissure, if the superior laryngeal nerve be uninjured, but if that nerve be divided on both sides, the glottis may be irritated with impunity. It is plain then that the inferior laryngeal is the principal motor nerve of the larynx, and that the superior laryngeal is at once its sensitive nerve, and the excitor of the motor action of the inferior laryngeal through the medulla oblongata.

It is scarcely necessary to remark how untenable is the opinion advocated by Majendie, that an antagonism exists between the superior and inferior laryngeal nerves, the one acting upon the constrictors, the other upon the dilators of the larynx. The superior laryngeal nerve supplies, as we have seen, only one muscle, and the inferior, to which he assigns the office of opening the glottis, supplies those muscles which are the principal agents in closing it.

Impairment or destruction of vocal power is a constant accompaniment to injury or complete section of the recurrent nerve.

An interesting experiment of Dr. J. Reid illustrates the power of each laryngeal nerve respectively. When the inferior laryngeals were cut, the superior remaining in tact, a probe introduced into the glottis occasioned signs of pain and efforts to cough, without any contraction of the glottis. But when the superior laryngeal nerves were cut, the recurrents being unimpaired, the probe could be introduced without exciting any irritation or effort whatever.

This experiment demonstrates unequivocally, that the spasmodic action induced in the larynx by the application of a stimulus to its mucous membrane must be referred to the class of physical nervous actions, and results from the influence of the superior laryngeal upon the inferior, through the connexion of their respective points of implantation in the nervous centre.

There can be no doubt that the motions of the œsophagus are regulated by the various œsophageal fibres given off from this nerve, in its course through the thorax. Irritation of its trunk has always produced contractions of the œsophagus, as testified by many experimenters. These contractions, Dr. Reid states, extended throughout

the whole tube to the cardia, where they became slow and vermicular; the œsophagus being shortened and diminished in calibre at each application of the irritant.

Distinct palsy of the œsophagus may be produced by section of the vagus in the neck. The following effects followed this experiment by Dr. Reid on a rabbit, which had been kept fasting for sixteen hours previous to the experiment. The animal eat a quantity of parsley, amid considerable dyspnœa and cough, with many efforts to vomit. It died in five hours. The œsophagus was found full of parsley throughout its entire extent down to the stomach, *which was also filled*, although not distended; and a good deal of the parsley had passed into the trachea and bronchial tubes, and even into the minute air-cells of the lungs.

The appearances in this experiment indicated complete paralysis of the œsophagus. This tube was filled by the propulsive power of the pharynx, which sent on morsel after morsel, until the whole stomach and gullet were filled, the latter being perfectly passive: and after these parts were occupied, and thus resisted the further passage of the parsley, it found its way more readily into the larynx and trachea.

It may be inferred from this and similar experiments that something more than an irritable condition of the muscular coat of the œsophagus is requisite in order to insure its contraction when distended by food.

The muscular fibres were quite uninjured, and, therefore, ought to have acted, if the stimulus of distension were alone sufficient to excite their contraction. The true cause of their inaction was the destruction of the nervous circle through which the sensitive nerves of the œsophagus could excite its motor nerves. This portion of the act of deglutition, therefore, is like that in the pharynx, a physical action, brought about by the impression of the food upon the sentient nerves of the œsophagus, which propagate their change to the centre where the motor fibres become excited. It cannot be said, however, that the mind is unconscious of this part of the act of deglutition, although it may be reasonably admitted that it has no necessary share in it.

The results of section of the cardiac nerves show that these nerves exert only a partial influence upon the heart: the destruction of them affects the actions of that organ only to a limited degree, inasmuch as the heart receives nerves from the sympathetic as well as from the vagus.

Numerous experiments demonstrate most unequivocally that this

nerve is of vast importance to the function of respiration. Section of one nerve produces no effect upon the respiratory organs, either structural or functional. Dr. Reid made careful examinations to ascertain if, after cutting out a large portion of one nerve, the lung of that side suffered any alteration in its texture, but he could not detect any. But when both nerves have been divided above the giving off of the pulmonary branches, the most severe dyspnœa comes on, the respirations are generally much diminished in number, the animal breathes just like an asthmatic; after a short time the lungs become congested and œdematous, and the bronchial tubes filled with a frothy serous fluid. When a piece has been cut out of each nerve or the cut ends of the nerves are kept apart, the animals never survive beyond three days, and during the whole of that period they suffer severe dyspnœa. If the cut ends of the nerves be kept in contact the animals will live ten or twelve days.

It may be inferred from Dr. Reid's experiments that section of the vagi nerves does not destroy that peculiar feeling of distress (*besoin de respirer*), which is occasioned by the want of fresh air in the lungs. He proved that animals, in which the vagi nerves had been cut, struggled violently, and seemed to suffer greatly, when the access of air to the lungs was cut off by compressing the trachea.

In such cases as that just described, the only channel through which sensitive impressions could be conveyed from the lungs to the brain is the sympathetic system, and it is to the afferent power of the sympathetic nerves and possibly to the same power in the cutaneous ramifications of the fifth and of the spinal nerves, that we must attribute the imperfect excitation of the respiratory act, which, under these circumstances, takes place.

The phenomena which follow section of both vagi are doubtless to be explained by the imperfect manner in which the centre of respiration is excited, after the destruction of the influence of these nerves consequent on their section. The movements, after the section, are partly of the voluntary kind, produced by the sense of distress occasioned by the imperfect supply. The asthmatic state which also follows the section may perhaps be in part caused by the irritation of the central portion of the nerve, exciting the medulla oblongata and the extremities of the motor nerves of respiration.

Lastly, the office of the gastric branches of the vagi nerves, appears from Reid's experiments to be chiefly to control the movements of the muscular coat of the stomach. Mechanical irritation of these nerves causes slow and vermicular contractions of this tunic.

Section of them may cause in the first instance vomiting and loathing of food, and it may retard the digestive process, but it does not put an end to it. For not only do animals, with the vagi cut, eat food from day to day, but, if killed at a sufficient period after digestion, their lacteals are found filled with chyle; affording unequivocal evidence of the persistence of the digestive process.

Nor does the section of these nerves destroy the secretion of the gastric fluid, for the matter vomited affords evidence of its having been mingled with acid, and the fact of the formation of chyle proves that stomach digestion must have taken place. Müller and Dickhoff, in their experiments upon section of the vagi in geese, found the fluid secreted by the stomach distinctly acid. In Dr. Reid's experiments, the ordinary mucous secretion of the stomach was found in its usual quantity, and when arsenic was administered to the animals, the mucous secretion was quite as abundant as in others in which the vagi nerves were not cut.

The few pathological facts which can be collected of diseased states of the vagi nerves are confirmatory of the conclusions deducible from anatomy and experiment. Several instances are recorded of loss of voice and dyspnœa, symptoms resembling those of chronic laryngitis, caused by the compression of the recurrent by an aneurismal or other tumor. The violent convulsive cough, which accompanies enlarged bronchial glands, is probably due to the irritation of the pulmonary branches of the vagi nerves. Hooping-cough is probably an affection of the vagi nerves by a peculiar poison. Dr. Ley attributed the phenomena of laryngismus stridulus to the irritation of enlarged cervical glands, affecting the recurrent nerves, and there seems no doubt, that, although the symptoms of this disease occur more frequently as part of a peculiar exhausted state of system, they may be, and are, produced sometimes by the local irritation of such glands.

The diseases in which this nerve is involved are chiefly those which affect its gastric and pulmonary branches. The sympathy which all practitioners admit to exist between the digestive and respiratory organs is explained by the anatomical relations of this nerve. Asthma is essentially an irritation of the centre of respiration and of this nerve; this disease almost invariably begins by some deranged state of digestion, or by the introduction of some poisonous material from without; some very subtle material suspended in the air, and brought by inhalation into contact with the respiratory surface, for example, the minute particles which pass off from powdered ipecacuanha, or from hay. Asthma and intermittent

fever often go together, because the marsh poison which gives rise to the one, may likewise excite the other. Asthma, which has occurred once, is easily reproduced by irregularities of diet, and consequent disturbance of digestion; and the frequent recurrence of the asthmatic paroxysm causes the dilated state of the air-passages and air-cells of the lungs, the dilatation of the right cavities of the heart, and the general displacement of that organ, which are invariably present in persons who have long been subject to this disease. Vomiting may be excited by irritation of the central or the peripheral extremity of this nerve. In disease at the base of the brain, vomiting is frequently an early symptom, being caused by irritation of the central extremity of the vagus. In sea-sickness the cerebral extremity of the nerve is irritated by the disturbance of the circulation in the cranium. By introducing emetic substances into the stomach, the vomiting is produced by the irritation of the peripheral extremity.

Many of the actions in which the vagus nerve is concerned are of the physical kind. Of these, œsophageal deglutition is the most marked. The closure of the glottis upon the application of any stimulus to its mucous membrane is another example of the same nature. But in both these instances and in all the movements with which this nerve has to do, sensation accompanies the act. In œsophageal deglutition, there is less sensation than in the other movements, but it is, nevertheless, present, particularly in case of any impediment being offered to the passage of the food. With reference to the movements of the glottis, it is interesting to remark, that whilst the will exercises a minuteness of control over them which is only surpassed by the power which it has over those of the fingers, it is only *closure* of the glottis which is caused by a physical stimulus. The obvious explanation of this is derived from the great preponderance of the constrictor over the dilator muscles of the glottis.

On what grounds Dr. M. Hall asserts that "the vagus nerve is certainly the least sentient of any in the class vertebrata,"* we are at a loss to discover. We do not hesitate to affirm that every act of an excitor kind, in which it is concerned, is accompanied by sensation, which in some is exquisite, in others feeble. Nor can we derive, either from the anatomy or physiology of this nerve, any confirmation to his hypothesis of a special series of excitor and motor nerves. It is well known that continued stimulation of the pharyngeal portion of the glosso-pharyngeal nerve upon the fauces will produce the feeling of

* The whole passage is "This nerve (the vagus) is certainly the *least* sentient, and the *most* purely excitor, of any in the class vertebrata."—New Memoir on the Nervous System, Adv. p. ix.

nausea, and even vomiting. Nausea is a feeling, accompanied by a particular condition of the muscular coat of the œsophagus and stomach, preparatory to vomiting, and may be produced by a certain degree or kind of stimulation of any part of the mucous membrane from the fauces to the stomach. The vagus, as well as the glosso-pharyngeal, is the instrument of this sensation; for the latter nerve has not sufficiently extensive connexions to justify the supposition that it is the sole agent. And this may be cited as a most striking instance of the sensitive endowment of the vagus.

The following conclusions may be adopted respecting this nerve and its branches.

1. That the vagus nerve contains filaments both of sensation and motion.

2. That its pharyngeal branches are motor.

3. That its superior laryngeal branch is the sensitive nerve of the larynx, containing a few motor filaments to the crico-thyroid.

4. That the inferior laryngeal is the principal motor nerve of the larynx.

5. That the cardiac branches exert a slight influence on the movements of the heart.

6. That its pulmonary branches contain both motor and sensitive filaments, and exercise an important influence upon the respiratory acts, for they cannot be destroyed without retarding materially the respirations, impeding the passage of the blood through the lungs, and causing œdema of these organs.

7. That its œsophageal branches are the channel through which the muscle of that tube are excited, through the medulla oblongata, to contract.

8. That the gastric branches influence the movements of the stomach, and probably in some degree the secretions and the sensibility of its mucous membrane; but that their integrity is by no means essential to the continuance of the secretion, or to complete chymification.

Of the Spinal Accessory Nerve.—The term *spinal* is applied to this nerve because of its extensive connexion with the upper part of the spinal cord. It escapes from the cranium along with the vagus through a common opening in the dura mater; but its roots are implanted in the side of the medulla oblongata, and of the cervical region of the cord as low as to the level of the fifth or sixth cervical nerve. On examining the side of the upper part of the spinal cord, the fascicles of origin of this nerve are seen emerging from it, in the interval between the ligamentum denticulatum and posterior roots of the spinal nerves. The lowest fascicles are those nearest to the

posterior roots of the lower cervical nerves. By the union of all the fascicles the nerve is formed, and it enters the cranial cavity from that of the spine through the foramen magnum.

Sometimes some of the upper roots of the spinal accessory nerve coalesce with the posterior roots of the suboccipital and the second and third cervical nerves. This appears to be nothing more than a junction of the fibres of two nerves which emerge from the nervous centre in close proximity to each other.

Very shortly after the escape of the spinal accessory nerve from the foramen lacerum, it divides into an *internal* and an *external* branch. The former coalesces with the vagus, where its second ganglion is formed, and, according to some physiologists, supplies the motor branches of that nerve; the latter passes outwards and downwards, through the deeper fibres of the sterno-mastoid muscle, to which it gives some branches, and anastomoses with branches of the second and third cervical nerves; and having crossed the triangular space in the neck between the sterno-mastoid and trapezius, it penetrates the latter muscle at its deep surface and is distributed in it, anastomosing with other branches of the cervical plexus.

We learn from the anatomy of this nerve that it supplies two great muscles, which play an important part in effecting certain movements of the head and shoulder, and, in a secondary manner, contribute to the actions of respiration, especially to those of a forced or extraordinary kind; and likewise that it forms a junction with the vagus nerve by a branch which consists of a considerable number of fibres.

There can be no doubt, from anatomy, that those fibres of the nerve which pass to the trapezius and sterno-mastoid muscles are principally motor, for their main distribution is to these muscles; and all experimenters agree in stating that, whenever stimulated, they excite these muscles to contract. Anatomy, however, equally indicates that these muscles derive motor power from branches of the cervical plexus likewise.

The office of the internal branch, which incorporates itself with the vagus nerve, is not so easily determined. Scarpa, Arnold, Bischoff, Bendz, and others, viewed it as contributing the motor fibres to that nerve, bearing to it the same relation as the anterior to the posterior root of a spinal nerve.

An objection to this view, although not an insuperable one, is suggested by the origin of the nerve, which seems more in accordance with that of the posterior roots of the spinal nerves than with their anterior roots, and this is especially the case with the lower fascicles

of origin which emerge from the cord quite close to the posterior roots of the cervical nerves. The reply to this objection is, that the external branch of the nerve is nevertheless distinctly motor, and that therefore the internal may be so likewise. Morganti and Bernard affirm that the lower roots form the external branch; if so, then the superior fascicles may be those which contribute to form the internal branch, and, therefore, its function probably differs from that of the external branch. We have already alluded to the fact that a coalition is sometimes observed between the posterior roots of the first or second cervical nerves, and the upper roots of the spinal accessory. The function of the former being confessedly sensitive, it is highly probable that the latter nerves, which are apt to coalesce with them, should perform a similar office.

To determine this question by experiment is extremely difficult, by reason of the small size of the internal branch and the great depth at which it is situate, which render it almost impossible to expose the nerve without injuring the vagus itself. Accordingly, we find the recorded statements of physiologists regarding the results of such experiments quite contradictory. The greatest number of observers, and the most recent ones, give their evidence against the motor function of the internal branch, at least against the doctrine of its yielding the motor fibres of the vagus nerve. Most of them, however, agree in stating that a degree of hoarseness and feebleness of voice always followed the section of the internal branch, as if *some* of the motor fibres of the laryngeal nerves were derived from it. From Müller's and Dr. John Reid's experiments, by irritation of the spinal accessory nerve within the cranium, no conclusive results were obtained favourable to the view which assigns motor power to the internal branch; on the contrary, these experiments rather tend to prove that the vagus contains within itself the motor fibres sufficient for the parts it supplies. These experimenters found that irritation of the trunk of the vagus, *before* its junction with the spinal accessory, caused contractions of the pharyngeal and laryngeal muscles, as well as of the fibres of the œsophagus.

Respecting the external branch of the spinal accessory nerve, it has been already stated that experiment confirms the results deducible from anatomy. We know that the trapezius and sternomastoid muscles receive nerves from the cervical plexus as well as from the spinal accessory. If the latter be cut these muscles are not paralysed, although weakened, and continue to act in respiratory as well as in voluntary movements, contrary to the views of Sir C. Bell, who regarded the spinal accessory nerves

as special nerves of respiration, whilst those of the cervical plexus were nerves of volition. There are indeed no good grounds for coming to any other conclusion than that which Dr. John Reid arrives at; namely, that the external branch of the spinal accessory exactly resembles in its functions, the branches of the cervical plexus with which it so freely anastomoses.

It may be fairly asked, however, why do the trapezii and sterno-mastoid muscles receive their nerves from a double source? The most reasonable reply to this is, that while the branches of the cervical plexus serve to connect these muscles with the centres of volition and sensation in the ordinary way, the external branch of the spinal accessory connects it in a more direct manner with the centre of respiration. Nevertheless, this branch, although especially implanted in that centre, is capable of obeying voluntary impulses, so long as the medulla oblongata maintains its normal relation to the centre of volition.

Thus, on the whole, we assign motor power to the external branch of the spinal accessory, but we see no good reason to subscribe to the opinion that its internal branch must be regarded as the *motor root* of the vagus. Indeed, we are much more disposed, for anatomical reasons, to regard the office of this branch as totally different. None of the views hitherto put forward respecting this nerve explain the object of its peculiar and most extensive connexion with the nervous centre; a connexion which in the larger quadrupeds is still more extensive than in man. Our view is as follows: the internal branch of the spinal accessory consists of *afferent* fibres, which, connected with the sensitive surface of the respiratory organs, pass towards the centre in the trunk of the vagus, but separate from that nerve to be implanted in a large extent of the respiratory centre. This mode of implantation of the spinal accessory nerve serves to bring the sentient surface of the lungs and air passages into immediate relations with the roots of all those nerves which animate the great muscles of respiration, the phrenic, the external thoracic, the cervical plexus, and the motor fibres of the spinal accessory and vagus nerves.*

* Respecting the subjects discussed in this chapter, the systematic works on descriptive Anatomy and Physiology may be consulted; also Sir C. Bell's, and Mayo's works, and Dr. Reid's Essays in the Edinb. Med. and Surg. Journal; Dr. Marshall Hall's writings; the Article "Par Vagum," in the Cyclopædia of Anatomy and Physiology.

CHAPTER XXI.

THE SYMPATHETIC NERVE. ITS ANATOMY AND FUNCTIONS.

Under the title of Sympathetic nerve is comprehended a great subdivision of the nervous system, which presents certain peculiarities of structure and of distribution, whereby it is strikingly contrasted with the strictly cerebro-spinal nerves.

It consists of an uninterrupted chain of ganglia, extending on each side of the vertebral column, from the first cervical vertebra down to the coccyx, and moreover extending upwards beside the cranial vertebræ, and occupying spaces between the bones of the cranium and those of the face.

The ganglia are on the whole rather less numerous than the vertebræ: in the dorsal region there is generally a ganglion for each vertebra. The continuity of the chain is preserved by cords of communication which pass from one to the other: sometimes two ganglia are, as it were, fused together; the chains of opposite sides communicate with each other at various parts in the plexuses of nerves which originate from them, and, in front of the coccyx, through a single ganglion (*ganglion impar*), which is situate in front of that bone; whether they communicate at the cephalic extremity, or not, is uncertain. Ribes has described a *ganglion impar* upon the anterior communicating artery of the circle of Willis, similar to that on the coccyx, and other anatomists regard the pituitary body in the sella Turcica as a ganglion of this description, a common point of union for the right and left sympathetic chains at their cranial extremities.

The sympathetic nerve has very much the same general arrangement in mammalia and birds as in man. In the former the cervical portion is closely associated with the vagus nerve by a sheath of areolar tissue, but without interchange of fibres, excepting at its upper portion. In birds the cervical portion exists only in the canal formed by the foramina of the transverse processes of the vertebræ. In the batrachian reptiles the sympathetic is disposed as in mammalia. In the chelonian reptiles its ganglia are few and the lateral cords small. In serpents it appears to want the distinct ganglia which exist in other animals; it is, however, continued down the spine on each side, having frequent communications with the vagus. Numerous plexuses occur in its course. In the larger osseous fishes the sympathetic is sufficiently distinct, as in the cod: it is also present in the ray; in both, but especially the latter, it is the abdominal portion which is

chiefly developed.* In the cyclostomatous fishes the sympathetic is said to be wholly deficient.

For the sake of description, the sympathetic in the human body may be divided into the following portions, 1. The Cephalic. 2. The Cervical. 3. The Dorsal. 4. The Lumbar. 5. The Sacral.

In comparing these several portions, we find that they have certain characters in common. Each portion consists of its proper number of ganglia, which seems in some degree influenced by the number of vertebræ in that region of the spine to which it belongs. The ganglia are connected by cords of communication, which are not mere nerves, but are true extensions of the ganglia in a cord-like form; so that each lateral chain might be described as a continuous ganglion, with swellings at certain intervals. From each portion certain sets of nerves may be pretty constantly traced: these are, omitting the cords of communication between the ganglia, 1. *Visceral* nerves, which generally accompany branches of neighbouring arteries to the viscera. 2. *Arterial* nerves, apparently devoted to arteries in the vicinity of the ganglia. 3. Nerves of communication with the cerebral or spinal nerves, which emerge from the cranium or spine near to the ganglia.

The visceral and arterial branches have a remarkable tendency to form plexuses, generally very intricate, which entwine around the blood-vessels, and, in the former case, are conducted by them to the tissue of the viscera.

The branches of communication with cerebral or spinal nerves, are among the most remarkable connected with this portion of the nervous system. We have already (p. 222, vol. i.) described certain of them as consisting very distinctly of two portions or bundles, one composed of tubular fibres, the other almost exclusively of gelatinous fibres. These bundles have been very commonly described as constituting the roots of origin of this nerve.†

On tracing back the gray bundle, connected with one of the spinal nerves, it is found that most of its fibres go to the ganglion of the posterior root of the nerve, some passing into the anterior root. A few of these fibres may be found in each root; they are not, however, traceable into the spinal cord, but seem to connect themselves only with the blood-vessels of that organ. Such is probably the anatomical history of the so-called gray root of the sympathetic connected with every spinal nerve. It may therefore be

* See Mr. Swan's beautiful Plates of the Comp. Anat. of the Nervous System.

† A good figure of these roots is given in Wutzer's work, "De Corporis humani gangliorum frabrica atque usu." Wutzer does not, however, distinguish them as white and gray. Berlin, 1817.

more justly regarded as a nerve originating from the sympathetic ganglion, which by some of its fibres connects that ganglion to the ganglion on the posterior spinal root, and by others is distributed to the vessels of the cord. This is the conclusion which Mr. Beck's recent researches have led him to adopt, and the careful examination of his very able dissections induces us to believe this to be the correct view.

The white root, or the bundle of tubular fibres, when traced to the spinal nerve, appears like a branch of it, i. e. a series of fibres, separating from it, and passing to the sympathetic. It derives fibres in nearly equal numbers from the anterior and the posterior root. In every instance it may be seen, spreading out upon the adjacent sympathetic ganglion, passing through its vesicular matter, and following the course of the trunk of the sympathetic for a longer or shorter way, and then proceeding from it in connexion with its gelatinous fibres chiefly to viscera. Mr. Beck informs us that he can, under the microscope, distinctly trace the continuity of these fibres *through* the ganglion, and he is of opinion that they do not form any organic connexion (as some fibres in ganglia and other nervous centres undoubtedly do) with the vesicles of the ganglion, beyond that which might result from passing between them. These fibres, then, according to this statement, must be regarded as a branch of the spinal nerve, distributed in connexion with gelatinous fibres derived from the sympathetic ganglion to viscera and other parts.

If this view of the anatomical relation between the sympathetic ganglia and the cerebro-spinal nerves be correct, it seems evident that the proper sympathetic fibres must be viewed as a separate portion of the nervous system, consisting entirely of gelatinous or nucleated fibres which originate in the vesicular matter of the sympathetic ganglia. These fibres, however, are accompanied in their course by tubular fibres, derived from the cerebro-spinal nerves, which pass over or through the sympathetic ganglia without forming any intimate connexion with them, and which are distributed along with the gelatinous fibres to viscera and other parts.

1. *Of the Cephalic portion of the sympathetic.* This portion of the sympathetic consists of ganglia, which occupy different parts of the head, and are connected with each other, and with the superior cervical ganglion. They are four in number:—

1. The ophthalmic ganglion. 2. The sphenopalatine, or Meckel's ganglion. 3. The otic ganglion, discovered by Arnold. 4. The submaxillary ganglion.

The *ophthalmic*, or *lenticular*, or *ciliary* ganglion is found in the orbit, situate on the outer side of the optic nerve, a little way before its entrance into the eye, enveloped in soft fat. It is a small quadrangular ganglion, of a reddish colour, not unlike a pellet of fat, for which it may be very readily mistaken by an inexperienced dissector.

Numerous nerves proceed from the anterior angles of this ganglion to the eyeball. These are the ciliary nerves, which have been already described, p. 40.

The ophthalmic ganglion is connected with the third nerve, and with the nasal branch of the ophthalmic division of the fifth. The branch of communication with the third nerve is a short thick nerve which comes from the inferior branch of that nerve: it is called by descriptive anatomists, *the short root* of the ganglion. From the nasal nerve proceeds *the long root*, a long and very delicate nerve, which attaches itself to the superior posterior angle of the ganglion.

We have not examined by the microscope the constitution of these branches of connexion with the third and nasal; but it is not uninteresting to notice that several anatomists have remarked in reference to them, that the place of each is occasionally supplied by two, which may answer to the two connecting nerves already noticed, in the dorsal portion of the sympathetic.

By means of a third filament called by some *the middle root*, this ganglion is brought into connexion with the cavernous or carotid plexus from the superior cervical ganglion.

The *sphenopalatine* ganglion is situate in the pterygo-maxillary fossa; it is a small, somewhat triangular, ganglion connected with the infra-orbital nerve, at its crossing over the spheno-palatine fissure, to pass along the floor of the orbit. This connexion is effected by two or three short nerves called commonly the spheno-palatine branches of the infra-orbital nerve.

From this ganglion proceed, first, *palatine* nerves, which are three in number (anterior, middle, and posterior), which pass through the posterior palatine canal, to be distributed to the mucous membrane of the hard and soft palate, and also to the nasal mucous membrane. Secondly, *nasal* branches, described by Scarpa, which enter the nose through the spheno-palatine foramen, and distribute branches to the spongy bones, and to the septum. One of these, the naso-palatine nerve, passes obliquely downwards and forwards, along the septum, and enters a canal in front of the foramen incisivum through which it passes to subdivide in the mucous membrane of

the hard palate. Thirdly, the *vidian* nerve, which coming off from the posterior part of the ganglion, passes through the vidian canal, and divides into two branches, the superior, or *the great superficial petrosal nerve*, which enters the cranium, and under cover of the dura mater passes through the hiatus Fallopii, to unite itself with the geniculate swelling of the portio dura;* and the inferior, or *carotid branch*, which enters the plexus around the carotid artery, and thus forms the bond of union between the spheno-palatine and the superior cervical ganglion; this latter branch is much the larger. Arnold states that this ganglion is connected with the optic nerve, and also with the ophthalmic ganglion.

The otic ganglion. This ganglion, discovered and described by Arnold, lies at the inner and inferior part of the inferior maxillary division of the fifth nerve, just at its exit from the foramen ovale. It is connected with this nerve by two filaments, which Arnold considers to be derived from the fibres of the lesser portion of the fifth nerve. Besides branches to the internal pterygoid, and the tensor palati muscles, it sends a filament into the cranium which passes through the hiatus Fallopii into the cavity of the tympanum, and there anastomoses with the tympanic branch of the glossopharyngeal. This is the *lesser superficial petrosal nerve*, which Arnold regards as an emanation from the glossopharyngeal, and as a root for the ganglion, analogous to the long root of the ophthalmic ganglion. The precise connexion of this ganglion with the sympathetic has not been clearly made out. It contains numerous gelatinous as well as tubular fibres, and its vesicles are large and distinct.

The submaxillary ganglion. This ganglion is occasionally replaced by a plexus of nerves. One or two fibres from the gustatory nerve constitute its roots, and its principal ramifications are distributed to the submaxillary gland. It is connected with the superior cervical ganglion through the cavernous plexus.

2. *Of the Cervical portion of the sympathetic.* This consists of three ganglia on each side, the middle of which is by no means constant. The *superior* is the largest, and extends from within an inch of the inferior orifice of the carotid canal, to the third cervical vertebra, and sometimes as low as the fourth or fifth. It is connected by large branches with the first, second, and third cervical nerves; from its upper extremity there passes upwards into the carotid canal a branch which divides into two that accompany the carotid artery, dividing

* It is probably from this source that this swelling receives the many gelatinous fibres already described.

and subdividing as they ascend, so as to form a plexus around that artery, *the cavernous or carotid plexus.* With this plexus numerous communications take place: there is one with Meckel's ganglion, another with the tympanic plexus; a branch to the ophthalmic ganglion, and one or two large ones to the sixth nerve, which formerly were regarded as roots of the sympathetic from that nerve; also one or two filaments to the third pair, and small branches attaching themselves to the ramifications of the carotid artery within the cranium. Communications exist between the superior cervical ganglion, and the several portions of the eighth pair, and the ninth pair at their exit from the cranium.

Inferiorly the superior cervical ganglion is continued into a cord of communication with the middle, or, when that is wanting, with the inferior cervical ganglion.

The arterial and visceral branches of the superior cervical ganglion, are, 1. The delicate gray nerves to the internal carotid artery, (*nervi molles* of Scarpa,) which, with branches from the glossopharyngeal, and vagus, form a plexus round the internal, external and common carotid arteries. 2. Pharyngeal branches, which, with filaments from the vagus and glossopharyngeal, form the pharyngeal plexus. 3. Laryngeal branches accompanying the superior laryngeal branch of the vagus. 4. A cardiac nerve, not always present, and very variable in size, (*the superior cardiac nerve* of Scarpa,) which either united with a similar nerve from the middle, or inferior cervical ganglion, or alone, passes along the carotid artery into the chest, to contribute to form the plexus of nerves belonging to the heart.

The middle cervical ganglion is very inconstant; it is placed opposite the fifth or sixth cervical vertebra, and besides the branches of continuation with the third, fourth, and fifth cervical nerves, it gives off one visceral branch, namely, the middle cardiac nerve, (*nervus cardiacus magnus* of Scarpa,) which is the largest of the three, and in default of the ganglion comes off from the intercommunicating cord. This nerve has a similar course to the inferior one; it is often absent, and its place is then supplied by filaments, which take a similar course, but are derived from the superior nerve, or from the vagus.

The inferior cervical ganglion. This ganglion is situate very low down in the neck, and is very deep-seated; it corresponds to the transverse process of the last cervical vertebra, to the head of the first rib, and is closely connected with the origin of the vertebral artery. It is frequently fused with the first thoracic ganglion, and is connected above with the middle, or, in its absence, with the

superior cervical ganglion. It is connected with the fifth, sixth, and seventh cervical nerves, and sometimes with the first dorsal.

The arterial and visceral branches of this ganglion are, 1. A nerve which accompanies the vertebral artery into the canal formed by the transverse processes of the cervical vertebræ. This nerve forms a plexus round the vertebral artery, and communicates with branches of the five lowest cervical nerves. There is no satisfactory evidence that this nerve passes up to the arteries of the brain. It seems chiefly a nerve to the vertebral artery, but doubtless also contains fibres from the cervical spinal nerves, which probably have a different destination. 2. The second branch of this ganglion is the third or *inferior cardiac* nerve which passes down, frequently in company with the middle cardiac nerve, to the plexus on the heart. 3. Branches which encircle the subclavian artery, in the first part of its course.

It is worthy of note that the most important visceral branches of the cervical portion of the sympathetic are destined to an organ, the heart, which is situated in the thorax at a considerable distance from their source.

3. *The Thoracic portion of the sympathetic* consists of a series of ganglia, corresponding, or nearly so, in number to that of the vertebræ; the ganglia lie upon the heads of the ribs, and are mostly small in size, and triangular in form. The first thoracic ganglion is often fused with the last cervical.

Besides the branches of communication with the spinal nerves, there are arterial branches which pass to the aorta, and there are also branches which pass into the pulmonary plexus.

But the most remarkable nerves which proceed from these ganglia, are the *greater* and *the lesser splanchnic nerves.*

The *great splanchnic* nerve arises by separate roots, probably from all the thoracic ganglia, more obviously from the fifth, sixth, seventh, eighth, and ninth; these roots unite to form a round cord, as large, if not larger, than the trunk of the sympathetic. This nerve passes alongside of the bodies of the vertebræ obliquely downwards and forwards, enters the abdomen by piercing the diaphragm, and ends in a large and complex ganglion placed by the side, and in front of the aorta, close to the origin of the cæliac artery; this is the *great semilunar ganglion.**

* The composition of this nerve deserves particular attention as illustrating the compound nature of the ramifications of the sympathetic. It may be regarded as the aggregate of a series of visceral nerves proceeding from the intercostal nerves, each of which, as it passes over the sympathetic ganglion immediately adjacent to the nerve

The *lesser splanchnic* nerve takes its rise by two roots from the eleventh and twelfth, or from the tenth and eleventh ganglia; it passes down in a similar course to the larger nerve, parallel to, and behind it, pierces the diaphragm, and unites with the renal plexus of nerves, and with the aortic plexus.

The striking analogy between these nerves and the cardiac nerves cannot fail to attract the attention even of the most superficial observer. The latter nerves, distributed to an important organ in the thorax, have their rise in the neck; and the splanchnic nerves, deriving their origin from nearly all the thoracic ganglia, are devoted to important viscera of the abdomen.

Of the Lumbar and Sacral portions of the Sympathetic. The chain may be followed down to the coccyx; the lumbar ganglia are small and irregular in number. The continuity of the chain between the lumbar and dorsal segments, is maintained sometimes by a small intercommunicating cord, between the last dorsal and first lumbar ganglion, which pierces the diaphragm, sometimes by a branch of the greater or lesser splanchnic, which of course establishes the continuity indirectly. The branches of communication of these nerves with the lumbar spinal nerves, are sufficiently distinct, and some of them are of great length. The gray branches are, according to Beck, larger than the corresponding ones in the thorax.

The nerves which come from the lumbar portion of the sympathetic are destined to the aorta, and to the lumbar arteries; the greater part of them form a plexus around the aorta, between the mesenteric arteries, from which proceed fibres to form the *inferior mesenteric plexus*, which follows the inferior mesenteric artery; below this artery the aorta is still embraced by a plexus, (*inferior aortic plexus*) which divides into the *hypogastric plexuses*, one on the right and the other on the left, which supply the rectum and bladder, the organs of generation, and the accessory parts. At the base of the coccyx, the sympathetic of the right side, anastomoses with that of the left by means of a branch passing on each side from the last sacral ganglion to a ganglion in front of the coccyx, which is called the *ganglion impar*.

from which it arises, becomes associated with some gelatinous fibres. Thus, while each intercostal nerve contributes certain tubular fibres, each thoracic ganglion contributes gelatinous fibres. Sometimes these two sets of fibres are kept distinct, and the splanchnic nerve consists obviously of a white and a gray portion. The gelatinous fibres are considerably more numerous at the lower than at the upper part of the splanchnic nerve, as pointed out by Mr. Beck, who very justly cites the fact as strongly confirmatory of the statement that these fibres arise from the ganglia. Phil. Trans. 1846, p. 224.

Of the Thoracic and Abdominal plexuses. So large a portion of the sympathetic is distributed to viscera in the thorax and abdomen, that it may not improperly be designated as the *visceral nerve;* for those organs, upon which the great processes which contribute to the nutrition of the body so much depend, derive their nerves mainly from this source, and whatever cerebro-spinal fibres they receive, are distributed to them in intimate association with the proper filaments of the sympathetic.

The plexuses in the thorax which derive nerves from the sympathetic are the pulmonary plexus, and the cardiac plexus.

The pulmonary plexus is chiefly formed by branches of the vagus, interlacing with each other from opposite sides along the median plane. It occupies two planes, one anterior to the bronchi constituting the *anterior* pulmonary plexus, the other *posterior*, which is much the more considerable and lies behind the bronchi. To these, but especially to the latter, nerves pass off from the higher thoracic ganglia.

The *cardiac plexus* is almost wholly derived from the sympathetic, only a few of its fibres coming from the cardiac branches of the vagi. It is very remarkable that all the nerves which the sympathetic contributes to this plexus, are derived from the cervical, and not from the thoracic ganglia. The plexus resulting from the anastomoses of these nerves, occupies an anterior and a posterior plane; the former passing in front of the great arteries, and following the course of the anterior coronary artery, in the anterior groove of the heart. The plexus entwines round this artery and its ramifications, and its fibres are doubtless conducted by them to the muscular fibres of the heart. The posterior plexus follows the course of the right coronary artery, and of its branches, which lies in the posterior fissure of the heart. A plexus of fibres, occupying a position intermediate to these plexuses, lies behind the arch of the aorta, above the right pulmonary, and sends a considerable plexus of nerves to the auricles. This plexus was described by Haller, as *the great cardiac plexus.*

Several small ganglia, or *gangliola*, are found in connexion with the nerves of the heart. Wrisberg described one just above the arch of the aorta, at the junction of anastomosing fibres from the superior cardiac nerves. A ganglion is also sometimes found in the plexus in front of the auricles, and Remak describes and figures several small ganglia upon the subdivisions of the anterior and posterior cardiac plexuses, and in the muscular substance of the heart.*

* Müller's Archiv., 1844.

The nervous plexuses in the abdomen are extremely complicated and numerous. They are principally derived from two great ganglia, situate on each side of the cæliac axis, in front of the aorta. These ganglia are semilunar in shape, convex downwards and outwards, they unite below the cæliac axis; and chiefly from their convex border, a vast radiation of plexiform nerves takes place, which follow the course of, and entwine around the branches of the cæliac axis, and of other branches of the aorta. To this great radiation anatomists have given the name of *solar plexus* and the conjoint semilunar ganglia must be looked upon as the great centre,—the sun of the abdominal sympathetic system.

Plexuses radiate from this source around the principal branches of the aorta, and they are named after the arteries which they accompany. They are the *diaphragmatic* or *phrenic;* the *supra-renal;* the *cæliac;* which divides into the *hepatic*, *gastric*, and *splenic;* the *superior mesenteric*, from which proceed nerves, which, with others from the lumbar portion of the sympathetic, form the *inferior mesenteric plexus;* and the *renal plexuses*, from which chiefly are derived the *spermatic plexuses*, destined to the ovaries in the female, and the testicles in the male. Of these plexuses the following are deserving a more particular notice:

The *gastric* plexus accompanies the coronary artery of the stomach, and passes along the lesser curvature of that organ. With the gastric branches of the vagus it forms the principal nervous supply to the stomach, which is completed by an off-shoot surrounding the right gastro-epiploic artery from the hepatic plexus, and by other nerves from the same plexus distributed chiefly to the pylorus, and by branches from the splenic plexus.

The *hepatic* plexus follows the hepatic artery and the vena portæ into the substance of the liver; it is joined by a branch of the vagus; and it gives off nerves to the stomach, and to the pancreas.

The *splenic* plexus surrounds the splenic artery, supplies the pancreas, and the left extremity of the stomach, by entwining round the left gastro-epiploic artery, and by direct branches to the great cul de sac of the stomach. These nerves then follow the branches of the splenic artery into the spleen.

The *superior mesenteric* plexus supplies the greatest portion of the intestinal canal, entwining round the superior mesenteric artery and its ramifications. Connected with it are some ganglia of variable size, called *cæliac* or *mesenteric ganglia*. From these ganglia, and from the upper part of the plexus, nerves are derived to the pancreas, and to the duodenum.

The branches of this plexus which pass between the laminæ of the mesentery do not accompany the smaller branches of the arteries so closely as elsewhere. They anastomose by arches, from which small branches pass to the intestine. The precise mode of termination of these nerves in the tunics of the intestines has not been ascertained.

In the pelvis we find a remarkably complicated plexiform arrangement of nerves distributed to the viscera of that cavity. These nerves are derived from the *hypogastric*, and from the *inferior mesenteric* (p. 138), and receive many fibres from the sacral nerves, which latter fibres are principally distributed to the pelvic plexus, a name given by Mr. Beck to an intricate anastomosis of nerves and small ganglia distributed to the rectum, bladder, and vagina. This plexus derives its nerves from the lower part of the hypogastric plexus, and from the branches of the sacral plexus.

A very important peculiarity of all the plexuses, wherever found, of the sympathetic nerve, consists in the presence of a quantity of vesicular matter in them, deposited in ganglia of very variable size, sometimes extremely minute, very rarely of great size, which are found scattered amongst them. These ganglia appear to give origin to gelatinous fibres. The plexuses, therefore, have the double office of intermingling fibres from different sources, and of affording points of origin for new nerve fibres.

Function of the Sympathetic Nerve.—In considering the function of this portion of the nervous system, it is of the utmost importance to pay close attention to the facts which the anatomical analysis of it discloses.

These facts are, that it contains a vast number of centres to and from which nerves proceed, and in which, it may be stated almost with certainty, gelatinous fibres originate: that in nearly every part of it two kinds of fibres exist, the gelatinous and the tubular; that the tubular are derived from the cerebro-spinal centre, the gelatinous from the sympathetic ganglia.

Two questions are to be solved in reference to the sympathetic.

1. Is the sympathetic a distinct and independent portion of the nervous system? or is it merely an off-shoot from the brain and spinal cord, exhibiting certain peculiarities of arrangement?

2. Do its fibres exhibit the same powers as those of cerebro-spinal nerves? that is, are they sensitive and motor?

I. No physiological question has been more amply discussed of late years than that of the relation of the sympathetic to the cerebro-spinal centres.

The view, which we regard as the correct one, rests entirely upon the facts of anatomy already stated. These facts lead us to consider the sympathetic nerve a compound nerve, consisting of gelatinous fibres, which are derived from the vesicular matter of the ganglia, and of tubular fibres, proceeding from the spinal cord. These fibres are bound together in the same sheath, and whatever be the proper function of each, they bear to each other a similar relation to that which the anterior and posterior roots of spinal nerves do in the compound nerve. Originating from different sources, and possessing probably different endowments, they travel in company to their several destinations.

We are aware that some physiologists of high and deserved repute altogether deny that the gelatinous fibres, which we have described as entering so largely into the constitution of the sympathetic, are nervous. They regard them as an early stage of fibrous or areolar tissue. The following reasons appear to us quite decisive of the nervous nature of these fibres. 1. They may be distinctly traced to the vesicular matter of ganglia; it is immaterial to the question whether they form their connexion with the sheaths or with the vesicles themselves, for we are as much at liberty to regard the nucleated envelope of the vesicles as a structure essentially nervous as the vesicles themselves. Parts of the encephalon appear to consist of little else than nuclei.

2. Throughout the sympathetic system these fibres and the tubular fibres exist in the several nerves in different but determinate numbers. Sometimes the two kinds are equal, sometimes one predominates over the other; sometimes the nerves consist solely of gelatinous fibres. Now if these latter performed the office of a sheath or support to the others, they would always be in due proportion to each other. Moreover, the gelatinous fibres would be alway outside, enveloping the tubular, which is not at all uniformly the case.

3. Nucleated fibres, very similar to the gelatinous fibres of the sympathetic, exist in parts where their nervous character is indubitable, as in the olfactory filaments (p. 8), and the nerve in the axis of the Pacinian corpuscle exhibits very much the same appearance, save that it is devoid of nuclei.

Adopting this view of the compound nature of the sympathetic, it is obviously impossible to regard it either as independent of the cerebro-spinal centres, or wholly depending on them. It seems probable that it is independent of them as regards its gelatinous fibres, but dependent on them as regards its tubular fibres.

And it may be stated that the views of anatomy which we hold

to be correct, justify us in affirming that the sympathetic exhibits marked indications if not of independence, yet of great peculiarity, in its mode of distribution. Clinging to the coats of arteries, it follows them for the most part in their ramifications, and attaches itself to them somewhat as ivy does to a tree. Yet of the mode of termination of the gelatinous fibres of the sympathetic, and of the nature of their relations with the elements of the tissues among which they lie, nothing certain is known; a fact attributable in a great degree to their want of such obviously distinctive characters as the tubular fibres possess. These latter, after leaving the blood-vessels, are probably distributed either to sentient surfaces or to muscles in the ordinary way.

The proper mode, then, of stating the reply to this question seems to us to be: that the sympathetic, taken as a whole, is not in itself a special and independent nervous system, but a portion of the nervous system peculiar in its composition, having, as regards some of its constituent fibres, a special relation to blood-vessels, particularly arteries, (and these are the fibres which are independent of the cerebro-spinal centres, having distinct centres of their own,) but being by others of its fibres connected, as all other nerves are, with the cerebro-spinal centres.

II. The second question affects the endowments of the constituent fibres of the sympathetic.

If we interrogate anatomy, we learn that the ramifications of this nerve are distributed to muscles as well as to sentient surfaces. The heart, for instance, derives its principal supply of nerves from this source. The intestinal canal between the stomach and the lowest part of the colon receives no nerves direct from the cerebro-spinal system, and is therefore dependent solely on the sympathetic, for whatever of sensibility it enjoys, or for such motor power as may be usually called into action by nervous influence. We, therefore, must infer from anatomy that the sympathetic contains both sensitive and motor fibres.

Many experiments lead to a similar conclusion. Stimulation of the cervical ganglia excites the heart to increased action; and irritation of the splanchnic nerves causes increased vermicular motion in the stomach and intestinal canal. Müller proved a similar result to ensue upon irritation of the cæliac ganglion. He exposed the intestines, and likewise the cæliac ganglion in a rabbit; he waited until the increase of peristaltic action, which exposure to the air always produces, had subsided, and then he applied potassa fusa to the ganglion, when immediately the peristaltic movements became

very vigorous. There is less agreement in the statements of the results obtained by different experimenters as to the sensibility of these nerves, as indeed is very commonly the case, when the question is respecting sensation; but the well-known occurrence of pain in parts supplied only by the sympathetic, is alone more conclusive as to the existence of sensitive fibres in that nerve, than the results of any experiment on a brute animal. How exquisite are the suffering of patients labouring under colic or the passage of a gall-stone, or of a renal calculus!

It is plain, then, that the sympathetic nerve contains both motor and sensitive fibres. An appeal to common experience shows us, that the latter cannot be very numerous, as parts supplied by the sympathetic nerve are not, in the healthy state, highly sensitive, and pain is felt in them only under the influence of great irritation. And with regard to the motor fibres, it shows that they are not at all, or at most to a very trifling extent, under the influence of the will. It is true that the will may be brought to bear upon muscles supplied by the sympathetic, by directing it simultaneously upon other distinctly voluntary muscles. This is well illustrated in the case of the iris; no effort, however great, if directed solely upon the iris, will cause that muscle to contract, but if the voluntary influence cause a simultaneous contraction of the internal rectus muscle of the eye, contraction of the pupil will take place upon each adduction of the eyeball.

It is highly probable that the increase in force and in frequency which takes place in the heart's action, during active exercise, is to be explained on the same principle; and that a strong effort of the will directed to the abdominal muscles, may excite an increased peristaltic action of the intestines.

Muscles supplied by the sympathetic nerve, although under ordinary circumstances referrible to the category of involuntary muscles, must not then be considered as absolutely and entirely removed from the influence of the will.

A very striking peculiarity, dependent in part probably upon the anatomical arrangements of the sympathetic, consists in the *rhythmical* nature of the movements of parts which derive their supply of nerves from this source, of which the movements of the heart and the intestinal canal afford good examples. And it is an important feature of these actions that they take place even when the parts are disconnected from the main portion of the sympathetic system. It is well known that the heart's action will go on for a considerable time after it has been removed from the body; and

that the peristaltic movements of the intestines will continue under similar circumstances.

This peculiarity seems to be referable to a double cause; first, the disposition of the muscular fibres themselves, which is such that a contraction cannot take place at one part without affecting the adjacent fibres, so that the contraction of one set of fibres appears to stimulate those in their immediate vicinity. This progressive contraction is well seen in the intestines. Secondly, the frequent occurrence of small ganglia, not only among the plexuses of the sympathetic, but also, as in the heart, upon or among the muscular fibres themselves. These ganglia, it is reasonable to suppose, are so many little magazines of nervous force, which, by their intimate connexion with the muscular fibres themselves, render them capable of repeating their action at intervals, after their disconnexion from the main trunk of the sympathetic system.

Much, however, in the peristaltic actions is perhaps due to the peculiar constitution of the unstriped muscular fibre itself; a constitution which gives it a slow and enduring, rather than a quick, energetic, and fleeting contraction. The actions of the heart are intermediate to those of the intestine and of voluntary muscle, and so are its muscular fibres, which, while they exhibit the striped appearance of voluntary muscle, are nevertheless devoid of the sarcolemma, and interlace in a peculiar manner with each other. The gelatinous nerve-fibres exhibit the same apparent inferiority of organization as the unstriped muscular fibre. It is a remarkable confirmation of these views, that in the tench (*Cyprinus tinca*), according to Ed. Weber, in which the muscular fibres of the alimentary canal are of the striped kind, there is no peristaltic action of the intestines, and that the application of a rapid succession of electrical shocks from a magneto-electric rotation instrument causes that sudden and quick contraction which characterises the striped muscular fibre.*

An observation made by Pourfour du Petit,† many years ago, suggested an office of the sympathetic, distinct from sensation or ordinary motion, but apparently not less important than either. He found that the division of the trunk of the sympathetic in dogs, op-

* By experiments with the magneto-electric instrument, E. Weber has given additional illustration of the fact that the peristaltic contraction is characteristic of the unstriped fibre, and that the sudden and quick contraction is peculiar to the striped fibre. See his elaborate article "Muskelbewegung" in Wagner's Handwörterbuch, 1846, and our remarks at pp. 185, 192, 193, vol. i.

† Histoire de l'Acad. Royal des Sciences, an. 1727, &c. Lettres concernant des reflexions sur les decouvertes faites sur les yeux, 1732.

posite the third or fourth cervical vertebræ, was followed, with remarkable rapidity, by a disturbance of the circulation in the eyeball; giving rise to a swollen and apparently inflamed state of the conjunctiva, a contracted state of the pupil, a flattening of the cornea, and a retraction of the eyeball, with protrusion of the fold of the conjunctiva, known by the name of the haw, and a flow of tears. Dupuy found similar effects resulting from the extirpation of the superior cervical ganglion in horses; and when the ganglia on both sides were removed, there were superadded to these more local effects, a general emaciation along with an anasarcous state of the limbs, and an eruption over the whole cutaneous surface.

Dr. J. Reid confirms these results of section of one sympathetic in the neck, as far as regards the eye, and he agrees with the other observers in stating that the injected state of the conjunctiva followed immediately after the section. In one case, he states that the redness of the conjunctiva took place *a few minutes* after the operation.

It has been already stated, that section of the branches of the fifth nerve, which supply the eye, is followed by ulceration and other signs of impaired nutrition in the eyeball. But these changes do not take place for some time after the section of the nerve; generally many days elapse: and they are attributable to the presence of irritating particles, which, owing to the insensible state of the conjunctiva are suffered to remain in contact with the surface of the eye, giving rise to inflammation and ulceration of its textures. The effects of section of the sympathetic are *immediate;* and are probably due to a change produced in the blood-vessels, in consequence of the withdrawal of their accustomed nervous influence.

The sympathetic thus appears to exercise a threefold office: first that of a sensitive nerve to the parts to which it is distributed; secondly, that of a motor nerve for certain muscular parts; and, thirdly, that of a nerve to the blood-vessels. It is almost certain that blood-vessels enjoy in their coats a power of contractility; and it seems highly probable that these nerve-fibres exercise an influence upon that contractility. Such an influence, it is evident, would materially affect the nutrition of parts the blood-vessels of which are subject to it; and, as secretion is mainly dependent on the normal nutrition of glands, it is reasonable to suppose that that function likewise would be to a certain extent controlled by these nerves.

It remains to enquire the sources whence these various classes of fibres in the sympathetic respectively derive their powers.

Looking to the anatomy of the nerve, there can be no doubt that some fibres are derived from the spinal cord or medulla oblongata, and that others proceed from the sympathetic ganglia. The motor and sensitive fibres, and some of those going to the other muscular parts, belong, no doubt, to the former class; the vascular, with the highest probability, to the latter.

Valentin's experiments indicate that the roots of the encephalic and spinal nerves exert considerable influence upon the movements of parts supplied by the sympathetic. For instance, irritation of the roots of the first three or four cervical nerves, excites increased action of the heart; and that of the dorsal and lumbar spinal nerves stimulates the peristaltic action of the intestines through the splanchnic nerves, and the abdominal plexuses.

The effects of diseased states of the spinal cord also afford a support, which is more to be relied upon than the previous experiments, to the opinion that the motor and sensitive fibres of the sympathetic are implanted in the spinal cord. When there has been extensive lesion of the cord, from injury or disease, the intestinal canal is always affected to a degree proportional to the extent of the lesion; and this affection shows itself in the torpor of the intestines, and the readiness with which they become distended by flatus, giving rise to the tympanitic condition of abdomen, which so generally attends disease or injury of the spinal cord.

It had long been thought that the sympathetic nerve plays an important part in the sympathies of the body. Our improved knowledge of the anatomical distribution of the nerves, and of their physiological anatomy, and of their endowments, clearly shows that the phenomena of sympathy are explicable, by the known laws of action of the great nervous centres, and that the sympathetic nerve can take no more prominent part in it than any other nerve; the extent to which it or any other nerve may be engaged in the play of such sympathies being proportioned directly to the extent of its central as well as its peripheral connections.

It would be more consistent, therefore, with a scientific nomenclature to discard the term *Sympathetic* as applied to this nerve; the old name *Intercostal* would, in some respects, be preferable. There is, however, great difficulty in finding a name which would adequately express its constitution and offices, which may be summed up as follows.

1. In its constitution it is compound, consisting of tubular fibres and of gelatinous fibres.

2. In its offices, it is a motor nerve to many of the internal viscera

of the body, the heart and the intestinal canal especially; it is also a sensitive nerve to these parts; and it presides over the actions of the blood-vessels of these as well as of other parts where it is distributed, as of the head and neck, and likewise of all the principal glands of the body.*

* On the Sympathetic nerve, consult Cruveilhier, Anat. Descr.; Valentin in Sœmmerring, Anat.; Longet, Syst. Nerveux; Lobstein, de nervi sympath. fabricâ, &c.; Valentin de function. nerv. cerebr. et sympath.; Mr. Beck, paper in the Phil. Trans. for 1846; Müller's Physiology; Bidder und Volkmann, die Selbständigkeit des sympathischen Nervensystems, Leipzig, 1842; Kölliker, die Selbständigkeit und Abhängigkeit des sypathischen Nervensystems, Zurich, 1844; Purkinje, in Müller's Archiv. for 1845, and translated in the Lond. Med. Gazette, vol. xxxvi., has described nervous ramifications which he considers to belong to the sympathetic, in the pia mater, dura mater, serous membranes, and other parts. Mr. Rainey also describes (Med. Chir. Trans. vol. xxix.) the arachnoid and subarachnoid tissue as consisting almost entirely of such nerves, a view which it is impossible for us to adopt. Much yet remains to be cleared up as regards the anatomical history of the sympathetic nerve in particular parts. Monographs upon the nerves of the heart, of the stomach, the intestines, &c. are great desiderata, founded on careful and minute dissections, by experienced anatomists, with the aid of the microscope. Further researches are likewise required on its distribution in the extremities.

CHAPTER XXII.

GENERAL VIEW OF THE FUNCTION OF DIGESTION.—OF THE MINOR FUNCTIONS WHICH CONTRIBUTE TO IT.—OF FOOD.—ITS QUALITY.—ITS QUANTITY.

Having discussed the great animal functions of Locomotion and Innervation, we now commence the consideration of those organic functions which are more directly concerned in maintaining the nutrition, and, consequently, the life of the individual.

Of the nutritive processes, the function of Digestion is clearly the most prominent and most important, inasmuch as it is that through which the animal is enabled to receive the aliment, and to prepare it for being assimilated to, and appropriated by, the various textures and organs of the body.

Under the general expression, "function of Digestion," must be comprehended several minor processes, all tending to the same object, namely, the reduction of the food for the nourishment of the body. The number of these subordinate processes varies with the degree of complication of the digestive function, which is obviously influenced by the complicated nature of the animal's body, and by the part which it has to play in the œconomy of the world.

Taking the digestive process, in its highest degree of complexity in man and the mammalia, we find that there is provision, first, for the *prehension* of the food; secondly, for its mechanical division and comminution (*mastication*), and for its admixture with a peculiar fluid (*insalivation*); thirdly, for the conveyance of the food into that portion of the alimentary canal in which its principal chemical changes are to take place (*deglutition*); fourthly, for the solution and reduction of the food preparatory to its being brought into a condition favourable to absorption (*chymification*); fifthly, for the separation of a material which shall contain in a condensed form the chief nutritive principles of the food, and which is easily absorbed into the blood (*chylification*); and lastly, for the removal of such portions of the food as have not been absorbed into the system during its passage along the alimentary canal (*defæcation*).

In examining the digestive process in the inferior classes of animals, various modifications are found to take place in it, according to peculiarities in the habits of

the animals, or in the nature of their food; and also according to the complexity of organization exhibited by them.

In *Mammalia*, modifications occur in the masticatory process; the vegetable feeder requiring a more complicated dental apparatus; the carnivora being provided with teeth of a simpler construction, but more fitted for seizing and lacerating the prey. In others again, the teeth are adapted to feed on insects, the Insectivora; in others, the Rodentia, certain teeth are constructed for gnawing dry and resisting substances; whilst in some of the whales, there are no teeth at all strictly speaking, but only an apparatus which will allow of retaining the finer kinds of food in their passage into the mouth of the animal. The other sub-processes of digestion are carried on very much upon the same plan as in the human subject, with only such variations as the habits of life of the animals may render necessary. Thus, in a large tribe of Mammals, the *Ruminantia*, the food is macerated in a complex stomach, prior to, as well as after, it has been subjected to a more complete mastication than is employed in any other animals. In these, as well as in all vegetable feeders, the intestinal canal is very long and capacious, and the cœcum of great size. In the Carnivora the stomach is simple, and the intestines short and narrow.

In *Birds* there are no teeth; and mastication, properly so called, is effected in the stomach, a portion of which (the gizzard) acquires a great increase of muscular power, and is lined by a dense cuticle, and thus becomes a powerful organ for triturating the food, the bird swallowing pieces of flint or other hard substances to aid the mechanical reduction. Insalivation is but slightly developed, excepting in the woodpecker, where very large salivary glands pour out a considerable quantity of saliva to aid the bird in picking the dry bark and wood of trees. In some birds, however, a dilated portion of the œsophagus (the *crop*) gives lodgment to the food for a time, and pours out from its mucous membrane a fluid which probably performs an office similar to that of the saliva, and which at least must serve to moisten the food before it passes further along the digestive tube. Chymification and chylification are essentially the same as in Mammals; and there are likewise similar differences as regards the length and development of the intestinal tube in carnivorous and herbivorous birds. In *Reptiles* the digestive process is, on the whole, simpler than in the preceding classes; but there are the same sub-processes, the alimentary canal being of a simple construction. The dental apparatus varies according to the mode of life of the reptile, (the fangs of serpents having evident reference to the predatory habits of that class of reptiles,) excepting so far as the beak may be regarded as a substitute; and in some, as the *chelonia*, it is entirely absent. In *Fishes* there are well developed teeth of various forms, and often very numerous, with a simple stomach and intestine, but no salivary apparatus.

In the *higher Invertebrata* the digestive process is carried on upon the same plan as in the vertebrata. In the *Cephalopods*, there are powerful instruments of prehension in the arms or tentacles which surround the animal's mouth and head. These animals enjoy a certain power of mastication by teeth, and some of them have a gizzard. All the *Mollusca* have a large liver; but other glandular organs connected with the intestinal canal, and more or less subservient to digestion, namely, the pancreas and spleen, are absent. The stomach and intestinal tube are very much as in the vertebrata. The *articulata* have also a digestive system like that in the vertebrate classes, but the liver is small, and developed in the rudimentary form of cœcal tubes opening into the intestine.

In the *lower Invertebrata* digestion becomes very simple. The intestine and stomach become much reduced in size; and in some the digestive apparatus consists only of a simple bag, as in the freshwater polyps, having the same orifice of entrance and exit; or, of a series of sacs or bags, with certain tubular appendages, as in the Asterias, and in the Actinia; in these latter animals one orifice answers equally for the introduction of the food, and for the discharge of the superfluous matters. In Medusæ, the oral aperture leads to a capacious cavity or stomach, from which certain canals carry the nutritious material into the different parts of the body, these canals being probably analogous to the circulating systems of the higher animals. In some polyps, the *Bryozoa*, as shewn by Dr. Arthur Farre, a portion of the stomach exhibits great muscular power, and seems to perform the fuction of a gizzard.

We shall find it convenient to examine the function of digestion by tracing it through the various stages, as above enumerated, describing the mechanism of each of the subordinate processes, and the change which each of them is capable of effecting in the food.

Before we enter upon these points, we must make some remarks upon the nature and quantity of the food suitable for the nourishment of man.

It has been already remarked at a former page (pp. 43, 44, vol. i.) that no food is suitable for the support of the human frame in a healthy state, but that which contains the great staminal principles, which are the chief constituents of the body. And the same remark applies with equal force to the carnivorous, and probably to the herbivorous classes of animals.

The food of the lower animals varies to a remarkable extent. But nearly, if not entirely, throughout the series, organized matter, either vegetable or animal, forms the proper nutrient material. It is probable that some of the lowest creatures enjoy the power of assimilating inorganic matter, and thus become the instruments of making the inorganic substances indirectly subservient to the nutrition of the higher animals.

The elements of nutrition for man, and the higher classes of animals, exist in the vegetable as well as in the animal kingdom. But some animals are so constituted, that in a state of nature, they subsist only on the flesh of other animals; while others live only upon vegetable food. Some carnivorous animals, however, may, in a state of domestication, be brought to eat vegetable food; but it rarely, if ever, happens that the herbivora can be taught to eat animal food. Man is, by nature, a truly omnivorous animal; and a certain admixture of animal and vegetable food is known, by experience, to be that which is most conducive to his healthy nourishment.

The classification of food which Dr. Prout has adopted, appears

to us to be eminently practical—and on that account we recommend it to the attention of our readers. As water enters so largely into the constitution of the body, being essential to the integrity and to the vital action of the solids, and as it forms the principal part of the blood, it is necessary that all animals should be supplied with liquid food in some shape. Accordingly, water, either alone or holding important nutrient elements in suspension or solution, forms part of the food of all animals—the *aqueous* group of alimentary materials of Prout.

A large number of substances derived from the vegetable kingdom, constitute the *saccharine* group of Dr. Prout. These are characterized by being composed of carbon, united to hydrogen and oxygen, in the proportions in which these latter elements form water; the proportion of the carbon varying from 30 to 50 per cent.* This group comprehends sugars, starch, gums, vinegar. These substances are contained in vegetables of various kinds, sometimes forming their principal constituent, and at other times combined with other nutrient principles.

The *oily* or *oleaginous* group of alimentary substances comprehends all those substances whose composition consists of olefiant gas and water. It includes the various fats and oils, as well as alcohol. It resembles in ultimate constitution the saccharine group; the proportion of carbon in the various substances contained in it varying from 60 to 80 per cent.

A fourth group, the *albuminous*, is made up of all those substances which contain nitrogen—such as fibrine, gelatine, albumen, caseine, vegetable gluten. All the materials which make up this group are derived generally from the animal kingdom, with the exception of the last, which is contained in great abundance in wheat; similar, if not identical, principles exist in vegetables. Wheat, indeed, consists of two substances—one referable to the saccharine group, the other to the albuminous, the forming consisting of starch, the latter of gluten. This fact was recognized more than a century ago (an. 1742) by Beccaria, who assigned the glutinous portion to the nourishment of the nitrogenous tissues of the body.†

In milk we find a natural combination of all the various substances employed for nutrition—and it is a fact of the highest interest that this product of animal secretion, elaborated for the nourishment of the young, should contain one or more substances for each of the above-named groups of alimentary materials.

* See Prout's papers in the Phil. Trans.

† Dr. Thomson, Med. Chir. Trans. 1846.

Thus, milk consists of water, sugar, oily matters (butter), caseine; and wheat, a substance of almost universal application for food, exhibits an analogous union of starch, the representative of the saccharine group—and of gluten, representing the albuminous.

It must be borne in mind that the albuminous aliments are distinguished from those of other groups by their containing nitrogen. Food of this kind is especially fitted to be directly assimilated to muscle, nerve, and the other animal tissues, into the composition of which nitrogen enters largely. These aliments contribute directly to the formation of the blood, from which the tissues attract the principles most proper for their nourishment.

The non-nitrogenous aliments are obviously fitted to nourish those textures which do not contain nitrogen, as the fat, or to supply those secretions in which carbon abounds, as the bile. Moreover, they furnish those large supplies of carbon which we are warranted in supposing the animal œconomy stands greatly in need of, not only from the great amount of that element which is to be found in all the tissues, but also from the large excretion of carbonic acid which is constantly taking place from the respiratory and other surfaces of the animal body. The formation of carbonic acid in the œconomy by the union of carbon and oxygen is, no doubt, the immediate cause of the generation of animal heat, and thus the supply of carbon in the food becomes of great importance to the maintenance of the proper temperature of animals.

From the natural subdivision of the food of man into two classes—one, consisting of the nitrogenized matters, well adapted by their constitution for the formation of blood; and the other, the non-nitrogenized substances, serving to supply a large amount of carbon, Liebig proposes to name the former *the plastic elements of nutrition*, and the latter *elements of respiration.*

To the first term we see no objection—but the use of any term which would imply that respiration must be, as it were, fed directly through the digestive process, appears to us scarcely consistent with the real facts of the case. The respiratory process is partly a process of supply, and partly one of depuration. It supplies oxygen, and it assists in the removal of effete matters in the shape of carbonic acid. The effete particles of the tissues would probably supply sufficient carbonic acid to effect the attraction of the required amount of oxygen—but as the supply of oxygen has the ulterior object of generating a due amount of heat, there will be required for this purpose a larger quantity of carbon than can be obtained merely from the destructive assimilation of the tissues (to use Dr. Prout's expression). Hence,

for this purpose, a special supply of carbonaceous material must be furnished to the blood—and this is derived from the non-azotized alimentary substances. We prefer, then, the terms lately proposed by Dr. R. D. Thomson, namely, *calorifacient* for the non-nitrogenized substances, *nutritive* for the azotized matters.

It is proper to notice that azotized matters may be calorifacient, inasmuch as they contain a large quantity of carbon; and it is known that large tribes of men live on animal food alone. A large number of North American Indians, according to Cattlin, live almost exclusively on the flesh of the buffalo, the only non-azotized food which they obtain being the fat belonging to it.

In determining the nature of the diet to be furnished in order to preserve man in a healthy state, care must be taken to provide for the calorific as well as the nutrient function ; and hence the admixture of a certain quantity of non-azotized food is needed for the former function. In the cold northern climates the natives instinctively feed on fat and oily food, which contains a large percentage of carbon ; while the natives of the warm south feed on fruits, which, as Liebig says, contain no more than twelve per cent. of carbon. Milk, the food of the young, in whom the production of heat ought to be most active, contains, according to Dr. Thomson, two parts of calorifacient for one of nutritive matter. Eggs also contain nutritive matter in a concentrated form, consisting chiefly of pure albumen, to which a considerable quantity of calorifacient matter is added in the oleaginous yolk. The accumulation of these substances, as a natural provision for the nourishment of the young, whilst yet under the sole guidance of the purest instinct, or, as in the egg, where the nutrient matter is directly absorbed by the tissues of the embryo, affords the surest indication that a compound food, consisting of such elements, is necessary for perfect nutrition at this period of life. As age advances, or the generation of animal heat becomes less active, the quantity of calorifacient food required is less, and that of the purely nutrient food more.

Experience justifies the conclusion to which our reasoning on these points leads, namely, that in the temperate climates the proper nutrient materials for infancy and childhood are milk, saccharine and amylaceous substances, the latter being combined with gluten; and that to these must be added a certain amount of gelatine, albumen, and fibrine, when the growth of the child and the more active play of its nervous and muscular systems calls for a further supply of nitrogenized food. In adult life, azotized substances are

needed, as a principal portion of the diet, to supply the waste which mental and bodily exertion gives rise to.

It must be confessed, however, that the views which theory suggests upon this subject are not such as would enable us with benefit, or even with safety, to determine the suitable diet for man. We learn much from instinct and more from experience, which we could never have gathered from *à priori* reasoning. Thus the importance of the admixture of vegetable with animal food could never have been determined without the aid of the experience afforded by the melancholy instances of disease generated by the privation of the former kind of aliment. Scurvy, as it is now well known, is frequently due to the want of a proper supply of fresh vegetable food; and it may be quickly and effectually cured by supplying this want. Again, it cannot be the deficiency of any of the staminal principles which gives rise to scurvy, because these exist in abundance in the animal food; and scurvy, it must be remembered, will occur in the midst of plenty of this kind of food. The disease is due to the deficiency of some unknown material necessary to health, which the vegetable kingdom alone can supply; and which, apparently, is most readily obtained from citric acid, lemon or lime-juice, or vegetables containing citric acid in good quantity, as the potatoe.

Nevertheless, the results of investigations as to the influence of particular kinds of diet in modifying nutrition, are strongly confirmatory of the views expressed above. Diet may be insufficient, either from its being given in too small quantity, or from its being defective in some principle, essential or incidental, necessary to the health of the blood—that fluid, upon the healthy condition of which the proper nourishment of the body depends. The effects of a diet scanty in quantity, although not objectionable in quality, are visible in the general emaciation, the wasting of all the tissues, and the consequent debility. If dissolution be slow, the great non-nitrogenized material of the body, fat, is employed to supply the animal heat, as is strikingly seen in hybernating animals. Specific effects follow the absence of certain elements of the food, even although the absolute quantity of it be abundant. If nitrogen be deficient in quantity, or altogether absent, the imperfect nutrition shows itself in the form of ulcerations of particular textures. Those tissues suffer most in which there is but little inherent activity of nutrition, or which are exposed to the contact of vitiated secretions. In Magendie's well-known experiments of feeding dogs upon sugar and water, the cornea of the eye ulcerated, and destruction of the

organ ensued upon the consequent evacuation of the humors. Similar cases now and then occur in the human subject from the supplies of nourishment being inadequate. Ulcers are very apt to show themselves on the mucous membrane of the alimentary canal; they will form in the mouth or in the intestine. These signs may be accompanied with a more or less scorbutic state, as shown in spongy gums, subcutaneous ecchymoses, &c., according to the extent to which the blood has suffered; they may occur, too, where there is abundance of fat, although wasting of muscles. If the supply of non-nitrogenous food be large, fat will be formed. When Magendie fed dogs exclusively on fat, there were ulceration of the cornea and wasting of muscle, but the tissues were infiltrated with fat. The case of the ill-fated Dr. Stark illustrated the effects of the long continuance of a diet deficient in nitrogen. This physician, with ill-directed zeal, dieted himself for four months chiefly on non-azotized food, water, butter, oil, sugar, taking only bread in small quantity, and meat or fish occasionally as azotized food. In a short time, well-marked scorbutic symptoms showed themselves without any diminution in the fat of his body; but subsequently diarrhœa, the result of ulceration of the intestinal mucous membrane, came on, and terminated his career.

Of the quantity of food necessary for health.—The proper quantity of food necessary for the support of general nutrition in a healthy state can only be determined by the results of observation and experiment; and the best mode of gaining information on this point is to consult the diet tables of various public institutions, in which due attention is paid to the health of the inmates, or to ascertain the allowances which are found sufficient for the army and navy. Each seaman in the British naval service, is allowed from 31 to 35½ ounces of dry nutritious food daily, of which 26 ounces are vegetable and the rest animal, the latter consisting of nine ounces of salt meat or 4½ of fresh. Sugar and cocoa are also given. The soldier is allowed a pound of bread and three quarters of a pound of meat. In most of the London hospitals, full diet, which is given to convalescent patients who need a liberal diet, consists generally of half a pound of meat, with from 12 to 14 ounces of bread, half a pound of potatoes, a pint of milk, and sometimes beer or porter, a pint of the former or half a pint of the latter. The former dietary is destined for men who must be in readiness for the most active athletic exercises, requiring not only great muscular strength, but also considerable power of enduring fatigue. The latter is intended to recruit the powers of those who have been suffering from disease.

If now we compare with these a dietary which has been found sufficient for the support of health in a state of more or less confinement, with a moderate amount of daily labour, we may fairly infer that the proper allowance for persons not engaged in actual manual labour lies between these extremes. In the union workhouses of England, able-bodied men obtain about 25 ounces of solid food daily, of which the quantity of meat does not exceed 5 or 6 ounces. In prisons it has been found necessary to give a certain amount of animal food to prisoners who are subject to hard labour. Each of such prisoners, if confined for a term exceeding three months and kept at hard labour, has a daily allowance of about 36 ounces of food, of which meat constitutes only a very small portion, namely, about 16 ounces in the week, four ounces on each of four days in the week. The prisoner has obviously the advantage of the poor man, whose only crime is poverty. But there is doubtless sufficient justification for this, in the fact that the labour of the prison, and the mental depression which long-continued restraint and confinement induce, render a greater amount of nutriment necessary than the indigent would require who seek in the workhouse a shelter from absolute want.

It is plain, then, that a daily amount of food, varying in quantity between 35 and 25 ounces, is sufficient to maintain health; but of this a fourth or a fifth ought to be animal food, especially when bodily exertion is being used. An amount greater than this is prejudicial, as affording material for the formation of new compounds, which serve only as *materies morbi* that may contaminate various tissues or organs, and impair their physical and vital properties. A lesser quantity, on the other hand, makes a poor blood, weakens the cohesive power of its elements as well as the attractive force of the tissues; and thus, in this latter case, *materies morbi* may be generated from the decomposition or the imperfect composition of the elements of the blood, and the tissues will suffer partly from not appropriating a sufficient quantity of the nutritious elements contained in the blood, and partly from the inferior quality of those elements themselves, which are probably also contaminated by some new compound.

In proportion as our knowledge of pathology or the intimate nature of disease extends, we become better able to treat disease with advantage on physiological principles; and it must be evident to all, who fairly consider the subject, that nothing is more important than to determine the proper diet suitable to particular maladies. We must not content ourselves merely with starving or feed-

ing a diseased person; but we must give him that kind of food (whether in large or small quantity) which his digestive organs can most readily assimilate, and which will not serve as pabulum to the morbid matter which is apt to be generated in his system. It is in diseases of the kidneys and liver that the most manifest good is derived from a well-directed dietetic system. In diabetes it has long been determined that a diet of animal food, with abstinence from sugar, and substances, such as starch, capable of being converted into sugar, is productive of excellent results. In diseases of the liver, more is to be gained by close attention to the quantity of the food than to the quality; at the same time that it must be borne in mind that a nitrogenized diet is more suitable than one abounding in carbon, which would throw upon that organ a work of elimination greater than it may be able to bear. In the rheumatic and gouty diatheses attention to diet is the main resource to counteract the tendency to generate the morbid agents which severally produce those states of constitution.

When there is a tendency to the accumulation of fat, a nitrogenized diet in regulated quantity is the most suitable to obviate it. When more carbon enters the system than is required for the calorifacient and respiratory functions, or for the nourishment of tissues, it will accumulate as fat: and it is only to be removed by the free admission of oxygen to consume it, care being taken at the same time not to favour further accumulation by the supply of too much food, especially of the non-azotized kind. The practice of trainers furnishes a useful commentary on this point, and may be imitated by many who suffer from dyspepsia. The following account of the system pursued in training was communicated to Sir John Sinclair by Mr. Jackson:—

"The diet is simple—animal food alone; and it is recommended to take very little salt and some vinegar with the food, which prevents thirst, and is good to promote leanness. Vegetables are never given, as turnips, carrots, and potatoes; but bread is allowed, only it must be stale. They breakfast upon meat about eight o'clock, and dine at two. Suppers are not recommended, but they may take a biscuit and a little cold meat about eight o'clock, two hours before they go to bed. It is reckoned much against a man's wind to go to bed with a full stomach, and they in general take a walk after supper. Some people will have tea; but it is not recommended, nor is it strengthening, and no liquor is given warm. Full and substantial meals are given at breakfast and dinner; beef and mutton are best. It is contended that there is more nourishment

in the lean of meat than the fat, which is fully proved by experiment, fat, being of a greasy nature, causes bile, and palls the stomach: the lean of fat meat is best. Veal and lamb are never given, nor is pork. The legs of fowls, being sinewy, are much approved of. The yolk of a raw egg is reckoned the best thing in a morning, and is supposed to prevent bilious complaints. Beefsteaks are reckoned very good, and rather underdone than otherwise, as all meat in general is; and it is better to have the meat broiled than roasted or boiled, by which nutriment is lost. No fish whatever is allowed, because it is reckoned watery, and not to be compared with meat in point of nutriment. The fat of meat is never given, but the lean of the best meat. No butter nor cheese on any account; cheese is indigestible. Meat must be dressed as plain as possible without seasoning of any kind. Men will live longer on beef, without change, than on any other kind of animal food, but mutton is reckoned most easily digested. The meat must always be fresh, and never salted. No quantity of meat is fixed; it depends upon the constitution and appetite. Little men will eat as much as large men, and very frequently more. Pies and puddings are never given, nor any kind of pastry; as to hard dumplings, people may as well take earthenware into their stomachs."

This system, it must be remembered, is combined with one of active and even severe exercise.

The periods for taking food, and the quantity to be taken, are under the natural guidance of certain sensations, which we call Hunger, Thirst, and Satiety.

Hunger.—The immediate cause of hunger cannot be explained. It is probably a sensation dependent on a peculiar condition of the mucous membrane of the stomach, which certain states of disease may blunt or may increase to an inconvenient extent, as in diabetes. The nerve which is instrumental in this sensation is probably the vagus nerve by its gastric branches, but there is no reason for denying to the sympathetic nerves, distributed to the stomach, some share in this phenomenon. The experiments of Brachet and Dr. John Reid, relative to the influence of the nerves on hunger, lead to no satisfactory conclusion, because of the difficulty of interpreting the sensations of dumb animals, and the probability that appetite would be destroyed or impaired after any serious operation, even although the injured nerve had nothing to do with the stomach. The sensations caused by extreme hunger would indicate that some further change was taking place in the wall of the stomach. A peculiar sense of sinking referable to the gastric region, general faintness,

secretion of gas into the stomach, and sometimes actual pain, accompany this state.

When these sensations are not relieved by their appropriate stimulus food, the effects of fasting begin to shew themselves. The body now feeds upon itself—in other words, the process of destructive assimilation is the only source from whence the blood derives its materials of supply. All the tissues shew the effects of impaired nutrition in the deficient manifestation of their vital powers—the animal loses weight, and, according to Chossat, this loss is most rapid the few days immediately preceding death. The tissue which wastes most is fat, and those which lose least are the osseous tissue and the nervous. There is also great loss of heat; Chossat states that the daily fall was half a degree of Fahrenheit; but on the last day it fell much more rapidly, reducing the temperature to 77°. The stomach is much contracted, and its mucous membrane thrown into thick folds or rugæ. The gall bladder is generally full to distension, the intestines are contracted like the stomach; according to Collard de Martigny, the lymphatics become full in the first ten days of fasting, but afterwards their contents decrease considerably. The respiratory movements become slow, and the pulse falls considerably in frequency. The urine becomes scanty, and all the parenchymatous organs are remarkable for their paleness. Furious delirium frequently manifests itself, when the loss of strength becomes considerable. A similar delirium sometimes ensues where too rigid an abstinence has been observed in the treatment of disease.

The period at which death occurs from protracted abstinence varies greatly; young animals die sooner than old ones. Dogs live from twenty-five to thirty-six days. In man, total privation is not borne above a week. By the aid of a little drink, given now and then, life may be prolonged considerably, and instances are recorded where it continued for eighteen or nineteen days, or even for thirty days. Dr. Willan saw a gentleman who voluntarily abstained from everything but water, flavoured with orange juice, for sixty days, and then died. Medical men, however, should exercise much circumspection in cases of professed abstinence, numerous impostures having been practised on this subject.

Thirst results from a peculiar state of the mucous membrane of the digestive tube, but more especially of the mucous membrane of the mouth and fauces, caused by the imperfect supply of liquid. A sense of clamminess in the mouth, pharynx, and even down the œsophagus, accompanies extreme thirst. The thirst in fevers is probably

due to the state of the blood and the consequent change in the secretions. Injecting thin fluids, as water, into the blood, relieves the thirst of poisoned animals, as found by Dupuytren and Orfila. Injecting liquids into the stomach relieves thirst, as was found in a case where the œsophagus had been wounded.*

* On the subjects of this chapter the reader may be referred to Dr. Prout's papers and works—Dr. Paris on Diet—Dr. Pereira's work on the same subject—Dr. Stark's works—Dr. Latham's account of the disease prevalent at the Penitentiary, 1825—Dr. Budd's lectures on diseases produced by insufficient nourishment, Med. Gazette—Sir John Sinclair's Code of Health, in which many interesting tracts relating to diet and regimen have been preserved — Tiedemann Physiologie, Band. iii. — Liebig's Animal Chemistry—Dr. R. D. Thomson on Food.

CHAPTER XXIII.

OF DIGESTION.—PREPARATORY PROCESSES; VIZ. PREHENSION, MASTICATION, INSALIVATION, DEGLUTITION: THE ANATOMY OF THE ORGANS CONCERNED IN THESE PROCESSES.*

In the present chapter we shall consider the preliminary stages in the function of digestion, under which head may be included all those which precede the entrance of the food into the stomach.

Of *Prehension*, or the taking of food into the mouth, little needs be said. It is performed chiefly by the hand, that wonderful instrument of man's lower instincts as well as of his higher attributes. The lips and cheeks, as well as the anterior teeth, and the tongue, are also concerned in this function.

The *lips* are endowed with great sensibility, derived from the superior and inferior maxillary divisions of the fifth pair of nerves, and are covered with largely developed papillæ of touch, which receive an abundant supply of blood from the coronary arteries. Along their margin the skin becomes continuous with the mucous membrane of the digestive apparatus, which, within these parts, as well as over the rest of the mouth, the pharynx and œsophagus, as far as

* In entering on a consideration of the alimentary processes, a few words may be conveniently introduced regarding the general anatomy of the *mucous system*, a term under which we include the skin, mucous membranes, and true glands, all of which are continuous with one another, and composed essentially of similar parts. The skin and the glands pertaining to it, as well as several parts of the mucous membranes, have been already minutely described in treating of the organs of sense. It only remains, therefore, to speak of the great internal mucous tracts, with their associated glands.

The *alimentary mucous membrane* commences at the lips, and lines the passages traversed by the food from the mouth to the anus. The principal glands whose ducts open upon it, are the mucous and salivary glands, the pancreas, and the liver. Besides these, its thickness is made up, in the stomach and small intestines, of an infinite series of tubular offsets, vertically arranged, pouring their contents on its free surface, and forming *an involuted or compound membrane*, or a diffused or membranous gland. The *respiratory mucous membrane* begins at the nostrils, sends processes to the olfactory, the optic, and the auditory organs, and lines the air-passages to their terminations; numerous mucous glands occur in this tract. Lastly, the *genito-urinary mucous membrane* commences at the genito-urinary orifices, lines the excretory passages pertaining to both functions, and is the essential consti-

the stomach, has an epithelium of the scaly variety; this variety forming the most essential character of that subdivision of the digestive apparatus considered in this chapter. The lips are moved by about twenty muscles, and are capable of grasping and retaining the food placed within them, and of aiding in the subsequent motions which it is made to undergo in the mouth. Their employment in articulation will be spoken of in another place.

The lips and the tongue undergo a variety of modifications in the animal series, with reference to the function of prehension; among these may be enumerated the enlarged, pendulous, and very moveable lips of the ruminants and solipeds, and of some monkeys. Man uses his lips in suction, as do the young of all mammalia, at the breast. Among fishes, the cyclostomatous group (as the lamprey) have a suction power of a similar kind, their circular mouth being surrounded and supported by a ring of cartilage, and furnished with appropriate muscles for producing adhesion to surfaces to which it is applied. In birds, the lips are modified so as to form the bill, which is always the prehensile organ in that class.

The tongue is used by man and animals in suction, somewhat as a piston, being drawn within the mouth so as to exhaust the anterior part of that cavity, and allow fluids to enter by the atmospheric pressure. The canine and feline races employ the tongue to lap fluids; the giraffe twines this organ around the leaves and branches

tuent of the glands of both. In the female, however, there is an exception in the case of the ovaries, as will be explained in a subsequent page.

Penetrating into all the recesses of the mucous system, and forming its chief bulk, we find *nucleated particles,* arranged as a layer, and developed in succession, in such a manner that the old ones disappear, while others advance from below. An *epithelium* is not peculiar to the mucous system, but is met with also on serous membranes, and on the walls of the blood and lymphatic vessels, as well as elsewhere; but it is distinguished here by its external position as regards other textures, so as to be capable of passing from the body, or to be exposed to the contact of foreign substances. The particles of this epithelium are very different in different parts, and may be divided into scaly, columnar, glandular, and ciliated. The *scaly* variety is seen on the skin, and in the alimentary tract as low as the stomach, as well as in the excretory parts of the genito-urinary tract. (See vol. i. pp. 404, 412, 437, &c.) The *columnar* variety consists of rod-like particles, placed endwise, generally bulged near the centre by the nucleus, and narrowest at the point of attachment. They are met with in the air-passages, on the intestinal villi, in the bile-ducts, and elsewhere. The *glandular* variety is bulky, its particles rather globular than flat or long, and found in all the glands, the several secretions being essentially the contents or substance of the particles set free. The *ciliated* particles are columnar or sub-globular in shape, but clothed on their free margin with cilia, as in the examples formerly figured, (vol. i. p. 62, and antè, p. 4.) They are found chiefly in the respiratory tract, and in parts of the genital tract of the female. The true scaly and glandular varieties of epithelium are never ciliated. See Cyclop. Anat., art. *Mucous Membrane.*

The

of trees, and detaches them with force. The ant-eaters have a remarkably long tongue, covered with a slimy secretion; this they protrude, and upon it entrap their victims. The chameleon among reptiles, and the woodpecker among birds, have each a tongue enormously developed for the purposes of prehension: to these many other striking examples might be added.

The cavity of the mouth, in which *mastication* is conducted, is bounded, first, by the palate or roof of the mouth, a fixed and hard surface formed by parts of the upper maxillary and palate bones, supporting a dense fibrous structure, lined with closely adherent mucous membrane, and fitted to act as a resisting surface against which the tongue may press the food; and, secondly, by the cheeks, lips, and tongue, which, in reference to the present function, may be classed together as tactile and muscular organs, designed to *handle* the food while subjected within the mouth to the action of the teeth, and then to forward it into the pharynx. Projecting into the mouth, above and below, is an arched series of teeth, or grinding organs, firmly fixed by roots into the alveoli of the upper and lower maxillary bones. Those of the upper jaw are immoveable, or only moveable with the entire head; but those of the lower jaw are capable of up-

The epithelium rests for the most part on a layer of membrane, hence termed *basement membrane*, which, in the best-marked examples, is distinctly homogeneous and transparent, but in some situations is finely fibrous, and not easily separable from the areolar and other tissues which lie below it. These two, the epithelium and the basement membrane, may be regarded as the constituents of a *simple mucous membrane*, although the latter cannot be everywhere traced, for example, in the interior of the hepatic lobules. The office of the basement membrane seems to be in all cases to sustain the epithelium, and to shut in or cover over those tissues which may be regarded as internal to the elements of the simple mucous membrane. Professor Goodsir considers that the basement membrane is covered with points, which he terms centres of nutrition, from which the development of the particles of epithelium proceeds; but we cannot accede to this view; first, because the best examples of basement membrane display no such points; and, secondly, because such a supposition does nothing to explain the successive growth of the particles.

The tissues which lie under the simple mucous membrane, as now sketched out, are areolar tissue, blood- and lymphatic vessels, and nerves, and in some situations a peculiar papillary tissue. These, in their several forms and proportions, greatly modify the characters of the membrane, as it is presented to the naked eye, and contribute largely to our common notions of the structure of the skin, mucous membranes, and glands. The areolar tissue forms the *cutis vera* of the skin, (vol. i. p. 406,) and the corresponding part of the great mucous tracts; while in glands it is generally in much smaller quantity. The blood-vessels and other textures are modified in various ways, as will be hereafter noticed in detail.

ward, downward, backward, forward, and lateral motions, by means of the muscles of mastication acting on the bone in which they are implanted. By these motions of the lower teeth upon the upper, the food is comminuted. A more detailed description of some of the organs of mastication may now be given.

The *cheeks* form the outer wall of that part of the mouth which lies outside the teeth. Like the lips, with which they are continuous, they consist of a muscular stratum interposed between the skin and the mucous membrane of the mouth. They admit of distension and compression, and form pouches which receive portions of food escaping outside the teeth during mastication, and from which it is continually returned towards the inner cavity, to be submitted to the grinding action. This use of the cheek is well exemplified in cases of paralysis of the buccinator muscle, in which the food collects in the flaccid bag to which this part is then reduced.

The *tongue* is an important agent of mastication, and has been already spoken of as the seat of taste and of an exquisite sense of touch. By virtue of the latter it receives accurate impressions of the tangible qualities of the food, and of its situation in the mouth; and by its great mobility it is constituted the main instrument by which the food is moved within the mouth, so as to be effectually brought within the range of the masticating organs. The tongue rests upon the hyoid arch, to which, and to the concavity of the lower jaw, it is fixed by the muscles. It lies within the curve of the teeth, and is covered on its free surface with mucous membrane, which has been before described. The muscular fibres which compose this organ intersect one another in an intricate manner in its interior, but they all appear to arrive ultimately at its dorsal surface, and to be there implanted, in small sets or bundles, into the submucous stratum of dense areolar tissue, a good deal of fat being disseminated throughout, but especially in the intervals between the muscular bundles at their insertion. We refer to works on descriptive anatomy for the anatomy of these muscles. By their action the upper surface of the tongue may be made convex or hollow, or may be pressed forcibly against the roof of the mouth; the tip of the organ may be protruded or moved in any direction, and to any recess within the cavity where food might lodge, and the whole organ may be lowered or drawn back. These several actions are so performed as to exemplify, in the most perfect manner, the concert which has been already mentioned to occur between many muscular and sensitive parts.

Of the Teeth.—These, in the widest acceptation of the term, and in reference to the whole animal scale, are hard organs situated on

the inner surface of the digestive tube, fitted for comminuting the food previous to its being acted on by the gastric juice. In the higher classes they are of an osseous nature and fixed to bone, though not originally. Among the invertebrata, the echini are remarkable for their calcareous oral teeth, five in number. The mouth of the leech is armed with three serrated teeth, worked by muscles, which saw their way into the skin. In some insects the gizzard is armed with a very complicated system of horny teeth. In the stomach of the crustacea is a cartilaginous framework, with projecting teeth, moved by muscles, and capable of very powerful masticatory actions. Among the gasteropods, the bullæ have three stomach teeth; and others, as the Aplysia, a great multitude, of large size and of different forms.

True osseous teeth are found only in three classes of vertebrata, viz. mammalia, reptiles, and fishes. Some of these, however, are without them, as, among mammalia, the American ant-eater, the manis, the echidna, the proper whales; among reptiles, the tortoises; and the sturgeon among fishes. The teeth of fishes are fixed not merely to the maxillary bones, but also to the palate and other bones, bounding the mouth and throat, and they are often extremely numerous. The bills of tortoises and birds perform some of the functions of teeth; but in those of the latter class which live on hard vegetable substances, the muscular gizzard, with its hard cuticle, and by the help of small angular stones which the instinct of the animals teaches them to swallow with the food, performs the functions of a masticatory apparatus. Among the mammalia, the teeth are few in number, and limited to a single row in each jaw.

Teeth may be classed according to their shape and the function they have to perform. Thus, the following varieties may be briefly enumerated:—The cutting or gnawing teeth of the rabbit or beaver, —the front teeth of man. The conical teeth of fishes for seizing and retaining prey—the canine teeth of the lion and dog. The hinder teeth of the carnivora, with several sharp elevations for tearing. The more complex crushing teeth of the insectivora, and of the frugivorous monkeys. Lastly, the true grinding teeth of granivorous and graminivorous animals.

Of the Human Teeth.—The teeth in the adult human subject are thirty-two in number, of which four are incisors, two canines, four bicuspids, and six large molars, in each jaw. Those of the upper jaw form the larger arch, so as to overlap those of the lower jaw in front, and to overhang them somewhat at the sides, when the mouth is closed. Each tooth has a *crown* or *body*, projecting above the gum,

and a *root*, buried in the alveolus or socket; and the division between these is marked on the surface by a somewhat constricted line, termed the *neck*. Each tooth has also an internal *cavity*, containing a vascular and nervous pulp, and which is open only towards the root. Lastly, each tooth consists mainly of a peculiar modification of osseous structure, termed *dentine*, or *ivory*, which is coated over with calcareous *enamel* on the crown, and with a thin layer of true *bone* on the root. The position and shape of the several varieties of the human teeth are as follow:—

1. The *incisors*, or cutting teeth, are situated in front, (those of the upper jaw being the larger,) and present a single conical root of large size, and a vertical crown, bevelled behind so as to terminate in a sharp horizontal edge. These teeth are fitted for cutting the food. In herbivorous animals they crop the herbage, in rodents they are capable of gnawing even very hard substances.

2. The *canine* teeth come next to, and are larger than, the incisors, especially the root, which sinks deeply into the jaw, and renders the alveolar arch prominent by its size. This root is conical, and the crown more conical and less wedge-shaped than that of the incisors, being usually surmounted with a small pointed tubercle or cusp, whence they are termed *cuspidate*. In consequence of the small size of the lower incisors, the lower canines are nearer together than the upper, and fall within them when the mouth is closed. These teeth in the canine, feline, and other carnivorous tribes, are largely developed, and more decidedly formed for lacerating and tearing the flesh of prey.

3. The *bicuspids* or *false molars*, are not so large as the canines, which they succeed, but their crown presents two pyramidal eminences, as their name implies, and there is a tendency in their root to be double; this part being marked by a vertical groove, and its apex, sometimes bifid, being perforated by two apertures leading to the interior.

4. The *true molars* or *multicuspidate* teeth, are placed most posteriorly, and are distinguished by their great size, the square form of their crown, surmounted by three, four, or five cusps, a distinct neck, and by their shorter, but more divided root, which presents from two to five branches, the inner the more divergent, and each perforated at its apex. The hindermost of these are the *wisdom teeth*. The false, and especially the true, molars are admirably adapted for grinding and pounding the food, under the influence of those powerful muscles by which the lower jaw is moved in a lateral direction while being forced against the upper. Though the least

simple of the human teeth, these grinders are greatly surpassed in complexity of form and structure by the corresponding teeth of herbivorous animals, such as the ox, the horse, and the elephant.

The *internal structure of the teeth*, like that of bone, has been much illustrated by those modern microscopic investigations, which have introduced a new æra in the sciences of anatomy and physiology. The researches on this subject, opened by Purkinje, Fraenkel, and Retzius, and subsequently pursued with more or less originality and extent by Müller, Schwann, Tomes, Nasmyth, and especially by Professor Owen, have confirmed the almost forgotten discoveries of Leeuwenhoek, and brought the whole subject of dental structure and developement into clear and consistent light. We shall now give a short summary of the facts as they have appeared to our own minds, and refer, once for all, to the works quoted at the end of the present chapter, for information as to the share each inquirer has had in the general and very satisfactory result.

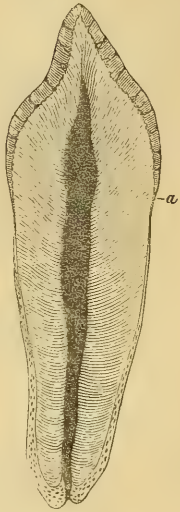
The three constituent substances, dentine or ivory, enamel, and tooth-bone or crusta petrosa, are found in all the higher and more perfect forms of teeth; and their several conditions in the range of animals have been greatly instrumental in leading to our present knowledge of them in the human teeth: our design, however, will allow us to speak of their character in the latter only, except in the way of illustration.

Taking a simple tooth as an example, (fig. 149,) we find the great bulk to consist of *dentine*, a term used by Mr. Owen to distinguish this substance from the rest, in preference to that of ivory or tooth-substance. The dentine gives the general form, size, and hardness to the tooth, both root and crown, and in its central part is the cavity containing the papillary substance or pulp, supplying the vessels and nerves of the organ.

Dentine is manifestly a modification of the osseous tissue. Like bone, it may be seen in favourable specimens to present a finely granulated ultimate texture, and, like bone, it is perforated by a series of minute channels, opening on the one hand on a vascular surface, (that of the pulp-cavity, which corresponds with the Haversian surface of bone: vol. i. p. 111,) and on the other sparingly branching, so as to permeate every portion of the tissue. The peculiarity of dentine consists chiefly in these internal channels of nutrition; and, as we have before shown the Haversian canals and systems of lamellæ in bone to be arranged in constant subservience to mechanical ends, so the corresponding parts in dentine, and especially those parts which answer to the lacunæ and canaliculi of bone, ap-

pear to derive their peculiar characters from the mechanical exigences of the case. The tooth having to sustain rude pressure on its crown, chiefly in a vertical direction, great density and compactness are requisite in its main constituent, and its internal vascular surface, which is small in proportion to the mass of dentine, is centrally placed, and receives its vessels and nerves at the deepest point, most remote from injury. As the vascular surface is small, and therefore at a great distance from a large proportion of the tissue, the interstitial channels of the dentine are capacious, especially towards the vascular surface, and comparatively direct in their course from it; and, instead of commencing minute as the canaliculi of bone do, and dilating at intervals, after a tortuous and irregular route, into hollow chambers, like the lacunæ of that texture, they are widest at their commencement in the pulp-cavity, retain throughout the simple tubular character, and are provided for the most part with proper walls; so that each tubule may be regarded as a hollow rod, the stem of which is of a harder and compacter nature than the intertubular substance through which it runs.

Fig. 149.

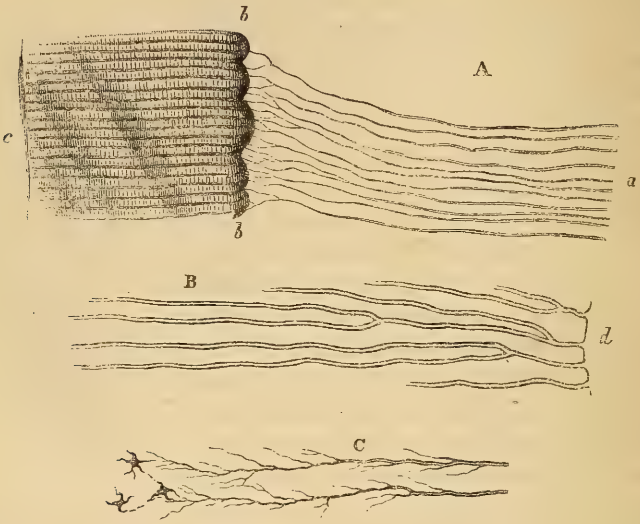


Vertical section of human incisor, shewing the general arrangement of its constituent parts. The dentine and pulp-cavity, the enamel on the crown, and the bone on the fang are seen. *a.* Neck of the tooth. Magnified 3 diameters.

The direction taken by the tubes is further interesting; for not only do they radiate on all sides from the vascular surface, as being the conduits of nutrition to the dentine, but they thus confer on every part of the tooth a greater power of resistance in an inward direction from the surface towards the centre, a power increased by the cylindrical shape of the pulp-cavity, and its tendency to an arched figure towards the crown. But it would appear that the beauty of the mechanical contrivance does not stop even here, for it has been observed that the tubes in many parts are doubly waved, like the Italic *ſ*, and that within these primary curves are comprised very numerous secondary meanderings; from which, as those of contiguous tubes have a lateral correspondence, a certain elasticity, and a greater capacity of resisting external force, must accrue. The tubuli of the dentine now described branch a few times dichotomously, and the branches retain for some distance the diameter of the trunk, this multiplication of their number enabling them

to occupy the spaces which would be left by the radiation of unbranched tubes from a common centre. The tubuli are in some parts about their own width asunder, in others they run in mutual

Fig. 150.



Sections of a human incisor, shewing:—

A. Junction of dentine and enamel near the neck of the tooth. *a.* Tubes of the dentine, dividing and ending on *b b*, the cupped surface on which the enamel rods vertically rest. *c.* Free surface of the enamel. The enamel rods are crossed by transverse lines and also by oblique dark lines.

B. Bifurcation of the tubuli of the dentine, soon after their commencement on *d* the surface of the pulp-cavity.

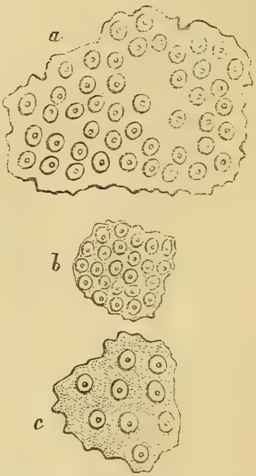
C. Branching of the tubuli of the fang, and their termination in the small irregular lacunæ of the "granular layer."

In these longitudinal views of the tubuli, their cavities only, and not their walls, are visible. Magnified 300 diameters.

contact; and their compact proper wall is about as thick as their cavity is wide. Except near the pulp-cavity, they are, as it were, hairy with filamentary canaliculi, which diverge on all sides, and form innumerable junctions with one another; so that the tubuli, throughout most of the dentine, may be said to communicate with each other independently of the pulp-cavity, into which they all open. Towards the outer surface of the dentine, where it is encrusted on the crown with enamel and on the root with bone, the tubuli gradually taper, and finally terminate in diminutive canals, which open, some into small, irregular lacunæ (forming a layer on the root, termed by Mr. Tomes the granular layer), some into the lacunæ of the osseous investment of the fang, and others upon the surface on which the enamel rests. Occasionally the tubuli are dilated into true lacunæ, or form free arches of communication.

The following facts illustrate the foregoing account of the structure of dentine. The granularity of the ultimate tissue may be best seen in specimens in course of developement. On the surface of the pulp-cavity the orifices of the tubuli can be seen; and in transverse sections of the tubuli,* (fig. 151,) their proper walls, the width of their walls and calibre, and their distance apart, are all discernible. In broken fragments, especially if torn after the tooth has been softened in acid, the tubuli may be observed to stand out from the surface, being broken off at different lengths, as if their structure was distinct from the intertubular tissue. Their hollowness is proved by the chasing of bubbles along them, visible under the microscope, when turpentine is added to a dry section, and also by the gas which may be seen to be disengaged in bubbles, chiefly from their interior, when a section is similarly treated with acid. The latter experiment seems also to show that the parietes of the tubuli contain a denser deposit of earthy matter, and are consequently harder and more resisting than the intertubular tissue. We do not regard the tubuli as filled up by solid contents, but as possessing a truly hollow bore, designed to give passage to fluids.

Fig. 151.



Transverse sections of tubules of dentine, shewing their cavities, their walls, and the intertubular tissue.
a. Ordinary distance apart.
b. More crowded.
c. Another view.
Human molar.—Magn. 400 diam.

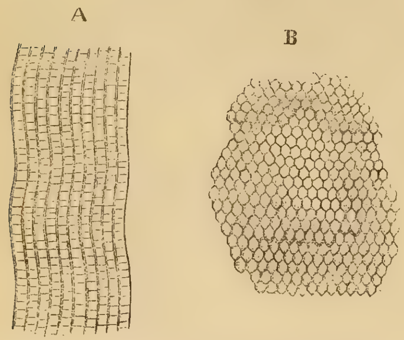
The *enamel*, investing the crown of the tooth, and forming that part which is exposed in the mouth to the contact of external substances, is harder and compacter than the dentine, and of peculiar structure, although formed, as will be afterwards shewn, on the same general plan as the other portions of organized bodies. As its earthy constituents are in much larger proportion than in the dentine, (for they make up 98 instead of 72 out of 100 parts, according to Berzelius,) the enamel requires much less nutrient change, and its interstitial passages are very minute.

The enamel (fig. 150, A, and fig. 152) consists of a congeries of hexagonal rods, placed endwise side by side, so as to form a layer, of which the surfaces are formed by the ends of the rods, and the thickness is determined by their length. The deep surface

* Mr. Topping, of York Place, New Road, mounts these and other objects very skilfully.

rests on the dentine, which presents a number of minute depressions for the reception of the deep ends of the vertical rods, a number of which rest in each; and the superficial surface, though said to be at first coated with a thin film of osseous tissue, is afterwards rendered bare by the earliest movements of attrition in masticating the food, and then becomes the free surface of the crown of the tooth. The rods of enamel are about $\frac{1}{4500}$th of an inch in diameter, and they pursue a more or less meandering course, which must augment their power of resisting external force. It is evident that their vertical position admirably adapts them to sustain pressure, and withstand the effects of force directed upon the surface of the tooth; while, at the same time, the interstices, or chinks intervening between them, principally at their angles of juxtaposition, are arranged in the most suitable manner for permeation by the fluids derived from the subjacent dentinal tubuli. These tubuli, indeed, may be seen to communicate directly with the interstitial passages of the enamel. The enamel rods are further marked, at pretty close and regular intervals, by cross lines, which, however, are far from constant, and of doubtful nature: some suppose them explained by the process of developement. The enamel rods are connected together by some remnant of the original organic matrix in which their earthy portion was at first deposited, and which is represented by the dark lines or chinks which appear to bound and isolate the rods. As the rods are placed vertically on the surface of the dentine, which is not an even one, they are not everywhere parallel or of equal length, but are truncated where they abut against each other over a hollow, and in such parts are most liable to decay. In many parts, however, near the dentine their vertical position seems disordered; they are curiously contorted, and neighbouring series of them are variously inclined, so as to lean against one another, while the same rods nearer the surface assume an upright and parallel course. The enamel on a vertical section further shews dark markings running obliquely across the fibres (fig. 150,

Fig. 152.



A. Vertical section of the enamel, shewing the fibres, with their cross lines.
B. Fibres of the enamel, seen endwise,
Magnified 350 diameters. From Retzius.

A), and not well understood, and also larger cracks or fissures (fig. 149), often branched, running through a part or the whole of its thickness. As Mr. Owen has pointed out, the enamel is the least constant of the dental tissues, being absent in many fishes, in existing ophidian reptiles, and in the edentate and many cetacean mammalia.

The *tooth-bone* or *cement* is disposed as a permanent thin layer of osseous tissue on the roots of the teeth, and it also invests the enamel with a delicate film on the first emergence of the tooth from the gum. On the roots it is thickest towards the apex, and often lines the pulp-cavity of the dentine for a little way in. It contains sparingly the lacunæ and canaliculi which characterise bone; and, when thick enough, it presents also the lamellæ of that structure. In general it is in too small a quantity to require special Haversian canals; but Mr. Tomes has shewn, that, between the roots of the larger human teeth, the tooth-bone is often in sufficient mass to be penetrated by a true canal of that nature; and, in the teeth of many animals, the cement is as vascular as ordinary bone. The canaliculi of the tooth-bone are for the most part directed from the lacunæ towards the surface, where the vessels are spread out, but a few communicate with the peripheral branches of the tubuli of the dentine. It is through this osseous investment of the roots that the teeth adhere so firmly to the sockets in which they are implanted.

The *cavity* of the teeth, containing the pulp, is in the fully formed tooth the analogue of the Haversian canal of bone, by which the organs of nutrition and sensation find access to the internal surface. The blood-vessels of the pulp are branches of the internal maxillary, and the nerves of the fifth pair, and they are both extremely abundant, in proportion to the extent of surface with which they are in relation. The capacious capillaries form numerous arches, and the nerves likewise end in loops, (vol. i. p. 221,) which are best seen in the young tooth. The white substance of the nerve fibres has seemed to us to be often diminished or lost towards the convexity of the loops.

The *alveoli*, or sockets in which the teeth are set, are cavities in the border of the jaws, corresponding in shape and direction to the roots of the teeth, formed on the outer and the inner side by a firm, compact, plate of bone, which bounds the alveolar arch in front and behind, and separated from one another by septa of less compact material. The surface of these cavities is spongy, being perforated by minute vessels, which pass across to the surface of the roots of

the teeth, and which there form a plexus in the substance of a firm elastic tissue, which is the connecting medium between the socket and the root, and is usually regarded as a periosteum. Thus the surface of the root is supplied with blood, and the tooth is united to the jaw in a way which allows it to yield very slightly under pressure.

The alveolar arch is covered on the outside by the *gums*, a dense, elastic, peculiar tissue, adapted to sustain without injury the forcible contact of the hard portions of food, to which its vicinity to the grinding organs must expose it.

The *developement of the teeth* may be described under two heads: first, that of the elementary tissues of the tooth, the dentine, the enamel, and the true bone; secondly, that of the dental series, which will include the order of appearance of the teeth of the temporary and permanent sets.

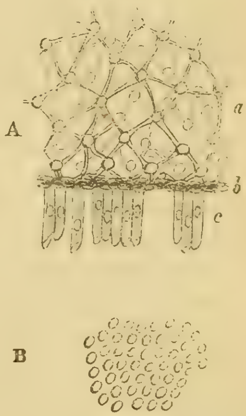
According to the most recent investigations of Arnold and Goodsir, the teeth are developements from the mucous membrane covering the dental arches, and not from the maxillary bones. They, therefore, would seem to correspond with the tegumentary appendages of animals, such as horns, nails, feathers, and not to be a portion of the true osseous system, or endo-skeleton of the vertebrata. The bills of birds are an obvious intermediate condition of the integument of the jaws.

The teeth may be regarded as formed in the following manner. The first indication observed (according to the excellent observations of Mr. Goodsir, which we have in most particulars had an opportunity of verifying) is a groove at the border of the palate in the situation of the future teeth, which he terms the *primitive dental groove*, and which is apparent in the fœtus of six weeks old. At the bottom of this groove there appear certain fine papillæ, which increase in size, and gradually assume the shape of the crowns of the future teeth, having the edge and cusps which are eventually to distinguish them. As the papillæ grow, the groove is converted into follicles for their reception, by the growth of septa between its borders, that is, between the outer and inner alveolar processes, which soon begin to be ossified within the walls of the groove. Thus the follicles become alveoli lined by the periosteum of the jaw, such as it is at this early period, and lodging a process of the mucous membrane of the gum, from the bottom of which springs up the papilla or germ of the future tooth. The summit of the papilla is at first visible in the mouth of the follicle; but ere it has assumed the figure of the tooth, the margins of the orifice enlarge

and lap over, and finally meet and unite, so as to form a lid or operculum to the now closed cavity. Thus the epithelium of the lining membrane of the mouth may be shewn to form the lining of the follicle, and to be reflected thence over the surface of the papilla.

Now, the tooth papilla must be regarded as homologous with, or answering to, the tactile and hair papillæ of the skin, already described at a former page: and it would, therefore, be expected that its main part would consist of a peculiar sub-mucous tissue, covered by a homogeneous basement membrane, and surmounted by a tissue answering to the epithelium; and this seems actually the case. The substance of the papilla is at first a congeries of granular nuclei, dispersed irregularly through a firm homogeneous sub-granular matrix, or blastema, in which vessels and nerves are by degrees developed. This is bounded by a definite transparent membrane, on which rests a reflection of the epithelium lining the sac, modified in structure, so as to present a series of columnar nucleated particles, the matrix of the future enamel. It would appear that the lining and reflected layers of the epithelium become blended together, and constitute but one, which is more adherent to the sac than to the papilla, so that on opening the sac its wall generally seems to be unattached to the surface of the papilla, and the latter to be limited by what we have regarded as the basement membrane. Or, it may be that the epithelium reflected over the papilla disappears, leaving only that which lines the sac.

Fig. 153.



A. Vertical section of the enamel-pulp, with the columnar epithelium, which is to become the enamel. *a.* Pulp. *b.* Position of basement membrane. *c.* Columnar epithelium, some particles being detached.
B. Columnar epithelium seen endwise. From a human fœtus of about five months. Magnified 200 diam.

Between the columnar epithelium thus lining the sac, and the surface of the alveolar cavity, that is, apparently in the wall of the sac itself, is now found a thick, semi-transparent, pulpy tissue, which has been termed *the enamel-pulp*. It presents towards the pulp of the tooth (dentinal pulp) a series of elevations and depressions, precisely the reverse of those of the dentinal pulp on which they rest, and answering mutually to these, with only the columnar epithelium intervening. The structure of this thick pulpy tissue is very beautiful and peculiar, as is seen in the annexed woodcut (fig. 153, A, *a*). It consists of a mesh of short fibres, meet-

ing in numberless points, and at each point of junction a transparent clear nucleus is visible.

It is elastic, spongy, loaded with fluid albumen, but destitute of vessels, and it seems perfectly distinct from that columnar structure which appears to be afterwards converted into the enamel.

In a vertical section of these parts, the enamel-pulp is seen covered with columnar epithelium, the *enamel matrix* (fig. 153, A, *c*, B), on the surface towards the dentinal or tooth-pulp; while, on the opposite surface, the blood-vessels of the membrane lining the alveolus are seen coming up to, and forming loops immediately under, the enamel-pulp, without penetrating it. It is further remarkable, that short tubes, filled with glandular epithelium, descend among these vessels from the enamel-pulp, and end by blind extremities. How these tubes, which are evidently glandular, can discharge their contents, it is difficult to understand, seeing they appear to open into the substance of the enamel-pulp: but their presence and precise situation we have ascertained to be as we have described them in the molar teeth of the nine months human fœtus.

It is not impossible that the enamel-pulp may perform the mechanical office of protecting the soft and growing tooth from pressure directed on the gum, and of providing a space in which developement may advance without restraint.

The next stage is that of ossification, and the earthy matter is first deposited in the homogeneous membrane forming the surface of the dentinal pulp. The most prominent portions of the crown are the first to harden; and the ossification proceeds inwards by the gradual conversion of the pulp into the dentine, or ivory. The nucleated particles of the pulp nearest the ossifying surface are found arranging themselves in series vertical to that surface; and it appears, that, in order to form these vertical series, they multiply by transverse division, much as those of bone cartilage are found to do. The earthy matters are then deposited in the indistinct cells surrounding the nuclei, so as to form the hard and dense walls of the dentinal tubes, as well as in the intercellular substance, so as to form the intertubular tissue of the perfect tooth. The cells unite endwise, and their nuclei elongate and coalesce in a manner to constitute the cavities of the tubes, and so as often to retain indications of this mode of origin in their permanent form. In all these processes a striking similarity to those noticed in the ossification of ordinary bone is to be traced. In proportion as the ossification proceeds inwards, so as to occupy the substance of the dentinal pulp, the vessels and nerves which had been developed in that structure recede, and finally come to occupy the cavity

which remains in the interior of the tooth after its developement has been completed. The chief vascularity of the pulp is uniformly found near the ossifying surface, whence it is evident that the earthy materials are supplied from that source. In the teeth of some animals, in which the dentine is penetrated by many subordinate offsets from the central cavity, containing blood-vessels, these passages are left in the progress of developement, just as has been above described.

It has been already said that the reflexion of the original mucous membrane of the follicle on to the papilla takes place at a line corresponding nearly to the *neck* of the future tooth, and that the original papilla answers to the crown or body of the tooth, and not to the root. This latter is a subsequent formation, and is laid down gradually after a certain amount of ossification has already taken place in the crown, and after the enamel has been calcified. It is formed and ossified by a process precisely similar to that of the dentine of the crown, only a more protracted one, and during which the tooth is raised out of its sac, and bursts the containing gum. The lengthening of the fang preceding its ossification resembles closely that occurring at the junction of the shaft with the epiphyses of the long bones during their developement (vol. i. p. 121.)

The calcification of the enamel commences on the surface of the dentine, in contact with that primary osseous sheet formed from the basement membrane of the dentinal pulp. On this primary layer are minute shallow cups, closely aggregated, answering to the ends of the enamel columns, and receiving them in a firmly cemented union, as the consolidation of the elementary cells proceeds. The enamel columns at a very early stage seem to consist only of a single series of nucleated particles, intervening between the dentine and the enamel-pulp; but subsequently others are added on the surface towards the enamel-pulp. Those of the new row arrange themselves endwise on the others, which they resemble in all respects, so that the enamel attains its proper thickness rather by the superposition of particle on particle, successively deposited, and by the subsequent calcification of each in its turn, than by the developement of its parts by an interstitial increase; and thus it appears to differ from the dentinal pulp, and to resemble the epithelium, to which it is allied.

It is from that surface of the enamel-pulp which looks towards the tooth, that this successive developement of new enamel columns proceeds; as they form, this tissue wastes; but it is not probable

that the pulp is converted into the columns, as the dentinal pulp is converted into dentine, because the anatomical characters of the pulp are so dissimilar from those of the columns. When first calcified, the enamel rods are loosely aggregated, and easily separate from one another under pressure; but they gradually become so firmly consolidated by the advance of the calcifying process in their interstices, as to make the finished enamel the most hard and indestructible of all the products of organization.

The developement of the layer containing the ordinary lacunæ of bone, and which, in the human teeth, covers the fang, and is continued a little way within the cavity of the root, does not seem to have been so accurately studied as that of the dentine and enamel. But this is the less important, as it is in all probability essentially similar to that of bone, which is now pretty well understood. There can be little doubt that a membranous matrix, probably like that of the cranial bones, is laid down as the fang is developed, in which the usual steps of ossification proceed, the lacunæ and their canaliculi being, in our opinion, formed from the corpuscles of the temporary matrix. Mr. Nasmyth has described a prolongation of this layer over the entire crown of the tooth, outside the enamel. To understand the formation of such a layer, we must suppose it laid down in a matrix continuous with that which invests the fang, passing over the crown between the enamel-pulp and the wall of the sac inclusive of the lids. The crusta petrosa in the fissures between the enamel of the compound grinders of herbivorous animals must certainly be formed in this way.

When the ossification of the dentine is so far advanced that the tooth can sustain with impunity the pressure to which it is destined, and when the enamel is densely calcified, the *eruptive stage* occurs, in which the tooth makes its way through the gum. This is due to the same laws of developement which govern the form and position of other organs. The gum over the sac is absorbed, and the crown of the tooth is forced upwards against it, chiefly by the increasing size of the fang below.

It may be stated, once for all, that, as the developement of the teeth proceeds, so does that of the alveoli, or the bony sockets in which they are lodged; and that, by the time the teeth break through the gums, their walls are sufficiently strong, and embrace the necks of the teeth with firmness enough to furnish a solid basis of support. Their vascular canals are developed, and especially those which convey to each tooth its interior supply of vessels and nerves. The gums and alveoli are likewise provided with vessels which play their

part in the developement and subsequent nutrition of the organs. The nerves of the teeth are derived from the second and third divisions of the fifth pair.

Of the First and Second Dentitions.—As teeth are required before the jaw-bones have attained their full growth, and yet are organs incapable of enlarging *pari passu*, with those bones, the young child is provided with a *temporary set*, commonly known as the milk-teeth, adapted to the size and form of its alveolar arches, and to the nature of the food consumed in early life. This set consists of twenty teeth—four incisors, two canine, and four molars in each jaw. They are formed in the manner already described: the papillæ of the anterior molars appearing first—between the sixth and seventh week of fœtal existence, according to Mr. Goodsir—followed by those of the canines, incisors, and posterior molars, about the eighth, ninth, and tenth weeks respectively. About the fourth month all these are in their saccular stage, the mouths of the follicles having closed; and there then appear behind the opercula, or lids of the follicles, small crescentic depressions of the mucous membrane, soon becoming closed cavities, called by the last-named author "*cavities of reserve*, to furnish delicate mucous membrane for the future formation of the pulps and sacs of the ten anterior permanent teeth" in each jaw. For two or three weeks longer the primitive dental groove behind the posterior milk molar is furnishing the papilla of the first permanent true molar; and as this becomes gradually in its turn enclosed in a sac, a cavity of mucous membrane is said, by Mr. Goodsir, to be left unobliterated between its sac and the surface of the gum, which is the "cavity of reserve" from which the developement, first, of the second true molar, and, secondly, of the third or wisdom tooth, is afterwards to proceed.

The temporary teeth usually make their way through the gum as follows, those of the lower jaw taking precedence: the four central incisors about the seventh month after birth; the four lateral incisors from the seventh to the tenth; the anterior molars from the twelfth to the fourteenth; the canines from the fourteenth to the twentieth; and the posterior molars from the eighteenth to the thirty-sixth month. This whole period is called that of the first dentition, and is of great importance to the child, from the various sympathetic morbid states which universal experience attributes to the process of "cutting the teeth;" but it would be beside our purpose to dilate in this place on so interesting and prolific a theme. It may suffice to say, that, in our opinion, the practice of lancing the gum over an advancing tooth is often unnecessarily and prematurely resorted

to, when there is no evidence, from its tense or inflamed state, that it is offering any undue obstacle to the progress of the organ beneath.

The ossification of the permanent teeth commences a little before birth with that of the anterior molars, and in the course of the first, second, and third years it proceeds gradually in the incisors, the canines, and bicuspids. Their position in the jaw, meanwhile, has been undergoing change. The cavities of reserve, from which the developement of the ten anterior permanent molars proceeds, are at first placed between the milk sacs and the gum; but as the papillæ are formed, as already explained, they recede behind, or to the inner side, and also pass deeper in the jaw, and ultimately get beneath them, acquiring by degrees their alveolar cavities, and being closely and somewhat irregularly packed. As the anterior molar is developed, it soon comes to occupy the tuberosity of the maxilla and the base of the coronoid process in the respective jaws, and, afterwards, by the lengthening of the alveolar arch, descends into place on a level with those before it. As this occurs, the cavity of reserve, situated over it, furnishes the papilla and sac for the second molar, which soon occupies the tuberosity or coronoid process, and then descends to behind the anterior one, a portion of the cavity of reserve being still left to furnish the hindmost molar or wisdom tooth in the same manner. As these several teeth descend to the alveolar arch, the jaw is proportionally lengthened by a suitable addition from behind; so that the circular arch, of which the alveoli at first consisted, is altered into an elliptical one.

As the permanent teeth are being prepared to penetrate the gum, the bony partitions which separate their sacs from those of the temporary teeth are absorbed; the fangs of the temporary teeth are removed by a very singular natural process; and the permanent teeth come to be placed directly under the now loose crowns of the temporary ones, which finally detach themselves and allow the permanent teeth to take their places in the mouth. While it is impossible not to admire the evidence of design furnished by this exquisite process, it seems sufficient to assign it physiologically to that general law which determines the form and size of the several parts of organized beings. It has been supposed that elongated productions of the cavities of reserve, which have been carried down from the surface with the permanent tooth-sacs, serve to re-direct them to their proper places as they rise through the gum. But it may be asked, what served previously to carry down the pulps aright, and to form these gubernacula? It is manifest that we must ascend to

a higher secondary law, to which to refer these wonderful phenomena of life.

The periods of eruption of the permanent teeth, though liable, like those of the milk-teeth, to some variety, are, according to Mr. Bell, usually as follow:—the anterior true molars at 6½ years of age, the central incisors at 7, the lateral ones at 8, the anterior and posterior bicuspids at 9 and 10, the canines from 11 to 12, the second true molars from 12 to 13, and the wisdom teeth from 17 to 19.

Of the Jaw-bones at different Ages.—The bones undergo some interesting changes of form in connexion with the growth and decay of the teeth, which have been well explained by Hunter. The alveolar processes in both jaws appear with the teeth, and disappear when no longer needed to support and enclose them. In the fœtus, before the eruption of the teeth, the upper gum is about on a line with the articulation of the jaw, the lower, consequently, is nearly on the same line, and the angle of the jaw very obtuse. But as the teeth protrude, and increase in number, the lower jaw is separated from the upper by the depth of the alveoli and crowns of the teeth of both jaws, the body and ascending ramus are both lengthened, and the angle approaches nearly to a right angle. When the teeth are subsequently shed, the alveoli disappear, and the lower jaw has to be much more elevated in order to touch the upper. But as its body and ramus cannot return to their former dimensions, its anterior part is thrown a good deal beyond the upper in this action, and it is only the hinder portions in the situation previously occupied by the molar teeth which come into contact.

Of the Articulation of the lower Jaw, and the Movements of Mastication.—A constant relation subsists in animals between the nature of the food, the shape and structure of the teeth, and the articulations of the jaw; so that, as Cuvier demonstrated, one of these elements being known, the others may be more or less accurately inferred. Thus, the purely carnivorous animals have teeth fitted to seize and lacerate their food, and the jaw is capable only of the simplest hinge motion. In the herbivorous families, on the contrary, teeth of a complex kind are provided for pounding and bruising the food, and the joints are so constructed as to allow of extensive sliding motions; while in all there is an inter-articular fibro-cartilage for protection under the extreme pressure exerted. The form of the articulation in man, not less than the dental series, denotes an intermediate condition, and forms a strong physiological argument for the mixed diet, which general custom and taste have decided to be natural to our species. As there are cutting, tearing, and grinding teeth, all in moderate proportions, of

similar height, and in an uninterrupted row, so the articulation of the jaw is intermediate between those of the animal and vegetable feeder. The transverse condyle is received into the glenoid cavity, and in the slighter movements of mastication and articulation does not leave it; but when the grinding teeth are used, or the mouth is opened wide, the condyle leaves the cavity, and slides forwards for nearly an inch on the prominent root of the zygoma. In the latter action the axis of motion is not in the condyles, but a little above the angle of the jaw, and the joint is arthrodial. A similar advance of the condyles may occur with the mouth nearly closed, the lower incisors being then carried to a level with, or even beyond the upper ones. By the advance of one condyle a partial rotation is effected, the centre of motion being in the other condyle; and when this is performed alternately by both sides, together with an elevation of the jaw, the lower molars are moved laterally over the upper, so as to powerfully grind any intervening substance. The temporal, masseteric, and internal pterygoid muscles more or less directly close the jaw. The hinder fibres of the temporal and masseter carry it also backwards, while the main part of the masseter, and especially the internal pterygoid, advance it. Both pterygoids carry it to the opposite side, chiefly by advancing its ramus, the centre of motion being then in the opposite joint. The external pterygoid neither raises nor depresses it. The depression of the jaw in mastication seems to be performed solely by the digastric; and it may be conjectured that even this muscle acts chiefly in its anterior belly, which, unlike the posterior, is supplied by the inferior maxillary nerve, the same which is distributed to the other muscles of mastication.

Of Insalivation.—The *salivary organs* consist of glands opening into the mouth and pharynx, and furnishing a peculiar fluid which is there mixed with the food and carried down with it to the stomach. The principal are the parotid, submaxillary, and sublingual; and to these may be added a multitude of small detached glands of similar structure, and probably yielding a similar fluid, scattered under the mucous membrane of the lips, cheeks, soft palate, and parts of the pharynx. The duodenal glands, comprising the pancreas and the glands of Brunner, which have much in common with the salivary glands, will be described at a subsequent page.

The salivary glands need not here be severally described. The parotid is remarkable for its proximity to the temporo-maxillary articulation, and some have attributed its greater activity during mastication to the pressure to which it is supposed to be then subjected; but besides that the fact of pressure may be doubted, so mechani-

cal an hypothesis seems quite superfluous, since the nervous sympathies which so evidently stimulate or control other secretions, as the tears, are quite sufficient to explain this. The parotids pour their secretions into that compartment of the mouth which is outside the teeth, while the ducts of the submaxillary and sublingual glands open under the tip of the tongue within the alveolar arches.

The salivary glands consist of a single excretory duct, continuous with the mucous membrane, branching again and again towards the gland, so as to subdivide it into a multitude of lobes and lobules invested with subdivisions of a common areolar or fibrous capsule, and reducible ultimately to follicles of a highly delicate basement membrane, lined by glandular epithelium, and provided on their exterior with a network of anastomosing capillaries. Some anatomists consider that the ultimate follicles of these glands, in which the secretion is elaborated, are at first closed sacs, in which the epithelium grows and is multiplied, and which discharge themselves at stated intervals into the extremities of the duct. Knowing how difficult it is to determine the positive truth on this question, we shall merely say that we are disposed to regard the secreting follicles as permanently open to the duct, and their secretory epithelium as a continuation of that which lines the duct.

Salivary glands exist in all the vertebrata except fishes.

The mere sight, or even the idea, of food to a hungry man, excites the salivary secretion—"makes the mouth water;" and during mastication it is poured very abundantly into the mouth, especially at the commencement of a meal, or if the food taken is of a savoury quality. Ordinarily, between meals and at night, these glands hardly pour out any secretion; but there can be little doubt that in these intervals of comparative repose of their blood-vessels, the epithelium of the follicles is undergoing those processes of growth and change which precede the actual formation of the salivary fluid; and the same may be said of many other glands which have an apparently intermittent action. The quantity of saliva furnished in a given time in a state of health has been variously computed. Mitscherlich collected between two and three ounces from the parotid duct in the course of twenty-four hours, and nearly fourteen from the whole of the salivary organs; and his estimate appears worthy of being relied on.

The *saliva* is a slightly viscid transparent fluid, depositing a little flocculent sediment on standing, which consists principally of the scaly epithelium of the mouth, and of other smaller nucleated cells,

which seem to come from the salivary glands or ducts. Its viscidity is increased by mixture with the mucus of the mouth. According to Dr. Wright, its specific gravity is, on an average, about 1007·9. It is usually alkaline, especially during a meal, but often neutral, and sometimes slightly acid. Less than two parts in a hundred are organic or saline matters, the rest is water. The organic matters are (besides the nucleated cells) ptyalin or salivin, fat, (often visible as oil-globules in the microscope,) and extractive matter, with a trace of albumen; the inorganic constituents are alkaline lactates, chlorides of sodium and potassium, phosphate of lime, some free soda, with sulpho-cyanide of potassium, and perhaps others. The last-named product gives a red tinge with a persalt of iron, and seems peculiar to the saliva. With regard to the nature and properties of what has been termed ptyalin, chemists appear to be by no means agreed, or even whether it be at all peculiar to this secretion. Dr. Wright, who has paid a great deal of attention to the saliva, describes it as a yellowish-white, adhesive, and nearly solid matter, having alone the characteristic odour of saliva, soluble in ether, alcohol, and essential oils, but more sparingly so in water; as unaffected by most of the agents which coagulate albumen, but as abundantly precipitated by subacetate of lead and nitrate of silver. Dr. Franz Simon, on the contrary, describes ptyalin as insoluble in alcohol and ether; and he adds, "Our knowledge of this substance is by no means accurate; and there is no doubt that all the animal fluids yield an extract to water, which strongly resembles, if it be not altogether identical with, ptyalin."* Dr. Miller has published a recent analysis of the saliva.†

An obvious use of the saliva is to aid in reducing the food to a pultaceous form, in which it is more easily swallowed. During the movements of mastication, it is intimately mingled with the whole mass, and may thus very probably mechanically enable the gastric juice to penetrate more quickly to every part on its arrival in the stomach. But general experience attributes the ill-effects of rapid eating or bolting of the food to the saliva being swallowed in insufficient quantity, as well as to imperfect mastication; and it is a question of some interest, to ascertain whether this fluid has any digestive powers, at all allied to those of the gastric juice. The experiments of Leuchs have proved that it has the power of converting starch into sugar, a change similar to that which occurs in the

* Animal Chemistry, translated by Geo. E. Day, (London, 1845,) p. 24.

† Cyclop. Anat., art. *Organic Analysis*, p. 812.

stomach; and Spallanzani observed that aliments enclosed in perforated tubes, and introduced into the stomachs of living animals, were earlier digested when previously mixed with saliva, than with water.

Dr. Wright injected saliva into the blood-vessels of dogs, and found the animals dying in a few days or weeks, with symptoms much resembling those of hydrophobia. In other instances, where he employed white of egg, isinglass, and mucus, no such effects ensued.*

Of Deglutition.—The parts concerned in this act are the mouth, the pharynx, and the œsophagus, the two latter of which remain to be considered.

The *pharynx*, as usually described, consists of all that cavity lined with mucous membrane which is situated in front of the cervical vertebræ, behind the nose, mouth, and larynx, below the base of the skull, and above the œsophagus. This cavity, however, as we shall shew, comprises two parts entirely distinct from one another: an *upper*, with its walls never in contact, lined with ciliated epithelium and containing air, which we shall term the *respiratory compartment*, being in fact strictly a portion of the air-passages; and a *lower*, dilatable and contractile, lined with scaly epithelium, and giving passage to the food from the mouth to the œsophagus, which we shall term the *alimentary compartment*, as it is a portion of the alimentary tube. The air-passages are interrupted between the upper compartment and the glottis, and in this interval the air has to traverse the lower or alimentary compartment in its course from the nose to the lungs. The alimentary and respiratory tubes may thus be said to intersect each other in this common cavity, a fact of leading importance to the understanding of the anatomical arrangement of these parts. Not to speak of the laws of developement to which this free communication of the two great tracts ministering to the nutrient function may be referable, (a communication still freer previous to the fusion of the sides of the palate at an early stage of fœtal existence,) it may be sufficient to allude to the great end answered by it, viz. the bringing the whole apparatus of the mouth into connexion with the lungs for articulation and speech, and to the subordinate object of much heightening the sense of taste during mastication, by allowing the odour of the food to ascend from the mouth and pharynx to the olfactory region through the posterior nares. (See vol. i. p. 446.)

* Lancet, 1844. Br. and For. Med. Rev., Jan. 1847.

From the hinder border of the hard palate passes *the soft palate*, a fold of mucous membrane enclosing mucous glands, a fibrous substratum, and several muscles by which it is capable of various motions. This terminates below by a free border, with the uvula in the centre; and from this border on each side descend the two pillars of the soft palate: the *posterior* downwards and backwards, enclosing and marking the course of the palato-pharyngeal muscle, and dividing the alimentary compartment before alluded to from the respiratory one above; the *anterior* downwards and forwards, containing the much-smaller palato-glossus muscle, and dividing the same compartment from the mouth. Thus, this alimentary tract of the pharynx may be said to have its upper part included within the diverging pillars of the soft palate, with the tonsils projecting into it, and to have its summit formed by the lower edge with the uvula, the posterior or upper surface of the soft palate pertaining to the respiratory tract, and the anterior or lower to the mouth. The mucous membrane of the pharynx seen between the soft palate and tongue on opening the mouth lies above the posterior pillars, and consequently belongs to the respiratory compartment; and we have on several occasions had interesting proof of this in those cases of chronic syphilis attended with a dry state of the pharyngeal membrane, and in which this part has remained dry after the patient has been made to swallow water.

The alimentary compartment of the pharynx has four orifices, all capable of closure: one towards the mouth, bounded by the lower edge and anterior pillars of the palate, by the base of the tongue and os hyoides; another towards the œsophagus, at the lower border of the cricoid cartilage: these two are alimentary. The third opening is towards the upper compartment, and is bounded by the lower border of the palate with the uvula, and by the posterior pillars with a portion of the posterior wall; the fourth is towards the lungs, and formed by the upper part of the larynx defended by the epiglottis: these two are respiratory. The shape of the alimentary compartment is very irregular, and capable of great alteration by the movements partly of the os hyoides and tongue with the larynx, and partly of the constrictor muscles forming its back and sides. Much lax areolar tissue, containing no fat, surrounds it, and allows of these movements on the contiguous parts. As it is impossible in the compass of this work to include a special description of the muscles and other constituents of the pharynx, we must suppose the reader to have already made himself acquainted with them from the ordinary sources.

The soft palate contains a thick layer of glands under its mucous membrane, in front of its muscles; and great numbers are situated about the upper orifice of the larynx and on the general surface of the pharynx. The *tonsils* are large and somewhat peculiar glands projecting between the arches of the palate. They open by several distinct orifices, which lead into cells, around which the secretory structure is arranged. They are very vascular organs, and evidently placed where they are to lubricate the food in its passage from the mouth. It is not, however, known with accuracy what is the nature or composition of the secretion they furnish; but it is, probably, little besides simple mucus. That it is not identical with the saliva may be inferred from the difference in structure of the glands, and from the tonsils being liable to inflammation and suppuration, as well as to strumous enlargement, while the salivary glands are seldom or never affected in the same way.

The food, when sufficiently comminuted and mingled with saliva in the mouth, and collected in the hollow of the tongue, is thrown into the alimentary pharynx by the tongue being pressed upwards against the roof of the mouth,—this movement beginning at the tip, and ending near the base. The division of the pharynx which is to receive it is dilated as the food enters, by the advance and elevation of the larynx, and by the yielding of its sides and posterior wall, while the communication with the respiratory compartment above is effectually closed by the coming together of the posterior pillars of the fauces, by the contraction of the palato-pharyngeal and upper constrictor muscles. The base of the tongue is now forced backwards and upwards, so that the pellet is pressed between it and the soft palate with its posterior pillars now in contact, and is thereby carried downwards and backwards into that portion of the cavity which lies behind the larynx. It crosses over the glottis without entering it, because while the larynx is advanced the base of the tongue presses back the epiglottis, and so covers the orifice; this movement of the epiglottis being assisted by the small aryteno-epiglottidean muscular fibres, and by the very course of the food itself; but it is abundantly proved, that even without an epiglottis the glottis would for the most part be so closed by sudden spasm of its constrictors, as to prevent any alimentary matters from falling into the larynx. In the act of vomiting, where the matters pass in the contrary direction, it is probable that the glottis is partly protected by the backward position of the tongue and epiglottis, and partly by this conservative contraction of the arytenoid muscles in answer to the mechanical stimulus of the food on the mucous mem-

brane in the vicinity. The pellet of food having arrived near the œsophagus, is projected into it by the contraction of the middle and inferior constrictors, the upper portion of that canal being dilated by its entrance.

It might be imagined that a process which may thus be artificially divided into consecutive stages, and which combines so many elaborate and harmonized actions, would occupy something more than a single second in its performance. It is, however, quite momentary. The movements cannot be performed separately by any voluntary control; the food once willingly thrown by the tongue beyond the isthmus of the fauces cannot be recalled, but is necessarily carried forward to the stomach—a beneficent provision, in which the physical supersede in a great degree the mental nervous actions, to ensure the integrity of the vital function of respiration. On the action of the nerves, however, we need add nothing to what has been already stated (see vol. i. pp. 333. 345, 346; and vol. ii. pp. 117. 120.)

The *œsophagus* is a tube continuous with the pharynx, fitted to convey the food past the organs of respiration and circulation in the thorax to the stomach below the diaphragm. It first lies upon the vertebræ and inclines slightly to the left, but afterwards, in its course through the posterior mediastinum, it advances in front of the descending aorta, and occupies the median line. It is surrounded in its whole length by a lax areolar tissue, which permits its dilatation and contraction during the passage of the food. It has a strong muscular coat composed of two layers, an outer, of longitudinal fibres, which commence from the cricoid cartilage; and an inner, of circular fibres: both these spread out upon the stomach, and become much thinner on that organ. The fibres of both layers are of the striped kind in the upper part and for a variable way down, some being often traceable as low as the diaphragm. In the middle region, unstriped fibres are mingled with the others; and in the lower part they are either the chief or only constituent. It has also a mucous lining, continuous with that of the pharynx and stomach, but different from both, being covered with a thicker and more opaque epithelium, resembling cuticle, and thrown, when empty, into longitudinal folds by the help of an abundant areolar tissue between the coats. Among the creases, chiefly in the lower third, are scattered mucous glands, which open on the surface, and serve to lubricate the canal during the passage of food. The cuticular lining of the œsophagus is changed abruptly at the cardiac orifice of the stomach into the glandular lining of the latter organ. Thus the œsophagus is organized as a simple conduit. It has con-

siderable muscular power, and a comparatively thick and insensible lining membrane.

On receiving the morsel forced into its upper orifice by the last act of pharyngeal deglutition, the œsophagus is mechanically dilated, and its lining membrane stimulated by the contact. The result is a contraction of its muscular coat upon the pellet, which is thereby carried forwards into the succeeding portions, in which the like actions are induced, until it has traversed the entire canal. This series of actions is rapid and quite involuntary, but an obscure sensation attends it, which is capable of being heightened to uneasiness or pain if any obstruction be met with, or if the descending morsel be too hot. It has been already stated that the contractions are due to a central stimulus on the muscular nerves, derived from the pressure of the food on those of the lining membrane (see p. 121). It has been pointed out by Müller that rapid and slight peristaltic descending contractions occur in the œsophagus independent of the passage of food. These are probably such as occur in the intestines and uterus, without the accustomed stimulus and as a mere consequence of their contractility. In vomiting, the œsophagus has an inverted action, the muscular coat forcing up the food thrown into it from below. In ruminating animals, this inverted peristaltic motion is capable of being accomplished by the will, and a similar power exists in some individuals among mankind, of which we have witnessed more than one striking example.

On passing a rapid series of electrical shocks down the œsophagus of a dog just killed, the upper three-fourths of the tube are thrown into continued or tetanic contraction, while the lower fourth takes on a peristaltic or vermicular contraction; thus demonstrating the situation of the change from the striped to the unstriped fibres of the muscular coat, according to the recent test of Weber.*

* On the subject of the teeth the student may conveniently refer to the works of Leeuwenhoek, John Hunter, Thomas Bell; Tomes, Med. Gaz. 1839—46; Owen, Odontography; Nasmyth, on the Teeth; Müller's Physiology, by Baly; Goodsir, Ed. Med. and Surg. Journal, vol. 51. On insalivation, he may consult Dr. Wright's works, which are of great interest and value. On deglutition, Dzondi's observations, in Müller, by Baly; a paper by Mr. Fergusson, in Med. Chir. Trans. vol. xxviii. p. 280; and the Cyclop. Anat., art. *Œsophagus*, by Dr. Johnson.

CHAPTER XXIV.

DIGESTION CONTINUED.—THE STOMACH.—ITS COATS, PARTICULARLY THE MUCOUS COAT.—STOMACH CELLS AND TUBES.—PYLORIC TUBES.—MOVEMENTS OF THE STOMACH.—THE GASTRIC JUICE, ITS NATURE AND PROPERTIES.—PEPSINE.—STOMACH DIGESTION.

The alimentary canal below the diaphragm is naturally divided into the stomach, the small intestine, and the large intestines, all of which are lined by mucous membrane, have, like the œsophagus, a double muscular coat, and are, besides, invested with a serous membrane, the peritoneum, which facilitates the motions by which the contained matters are propelled from end to end.

The stomach, of which we have first to speak, is an elongated curved pouch, very dilatable and contractile, fitted to receive the food from the œsophagus, to retain it while acted on by the gastric fluid secreted from the lining membrane, and then to transmit it to the duodenum or first part of the small intestine. It is expanded into an ample cul-de-sac at its left extremity, and becomes gradually narrower towards the pylorus, where it joins the duodenum. A circular constriction is often apparent three or four inches from the pylorus, partially dividing the pyloric region from the rest of the cavity. It has an anterior and posterior surface, which become respectively rather upper and lower during repletion of the organ (owing to its change of bulk, and its being fixed at its two orifices), and an upper and lower curvature, called also lesser and greater, which undergo a corresponding alteration, becoming rather posterior and anterior. The *peritoneum* invests both surfaces, and passes from them to the liver (forming the gastro-hepatic omentum), to the spleen (forming the gastro-splenic omentum), and to the transverse colon (forming first the anterior and then the posterior layers of the great omentum). This peculiar arrangement of the serous membrane is probably intended to allow of the extreme changes of bulk to which this organ is liable. The *muscular fibres* of the stomach are continuous with those of the œsophagus; but, in consequence of its irregular shape and its bulging from the cardia towards the left hypochondrium and the umbilical region, these

fibres are not regularly longitudinal and circular as in the œsophagus, and as in the intestines. The outer or longitudinal set may be best traced along the lesser curvature and near the pylorus; and those beneath cross them either at right angles or obliquely, according to their situation. Towards the lesser extremity the fibres of both layers are much thicker, and particularly so at the pylorus itself, where they form a circular constriction projecting the lining membrane, and capable of acting as a sphincter muscle. They are of the unstriped variety.

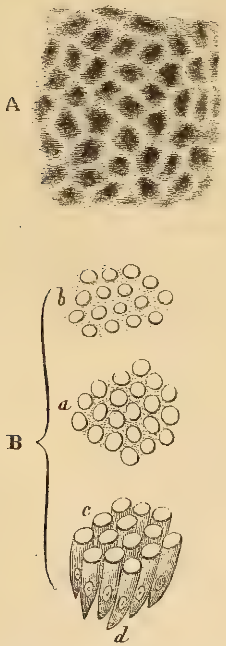
The *mucous membrane* of the stomach is thick and soft, and thrown into numerous irregular folds by the contraction of the muscular coat, except in the distended state of the organ. To be capable of this folding, it is separated from the muscular wall by a very lax areolar tissue, containing no fat, but filled with the vessels belonging to the mucous membrane, and also containing nerves. This is the coat wrongly styled nervous by the older writers.

The stomach is freely supplied with blood by the three divisions of the cœliac axis, the coronary, hepatic, and splenic. The branches of the arteries reach it along its borders, soon pierce its muscular tunic, and form plexuses in the sub-mucous areolar tissue, where they break up into numberless finer ramifications, which penetrate the mucous coat. The veins accompany the arteries in their distribution, and discharge themselves into the vena portæ. Both orders of vessels are very tortuous, and their contiguous branches everywhere anastomose freely, so as to distribute the sanguineous supplies equally during the changing volume of the organ. The nerves of the stomach are derived from the pneumogastrics and from the cœliac plexus. They advance from the lesser curvature over both surfaces, and after supplying the muscular walls, enter the areolar layer under the secreting lining membrane.

The mucous membrane of the stomach demands and will well repay an attentive study. It is of that variety which has been termed *compound mucous membrane*, i.e. its thickness is made up of an infinite multitude of tubular involutions of the simple membrane, with intermediate vascular, and other tissues sent up into it from below. The simple membrane consists of basement membrane and epithelium, both of which are found throughout. The vessels are uniformly on the deep surface of the basement membrane, and the epithelium on its opposite surface. The compound mucous membrane of the stomach is thinnest near the œsophagus, and is usually of a pinker colour in the middle region, and paler towards the pylorus.

Over the whole surface of the membrane as seen on laying open the organ, and stretching it so as to obliterate the larger folds, there are visible, even with the naked eye, but still better with a lens, a multitude of cavities of very irregular shape, and about $\frac{1}{200}$th of an inch in diameter, more or less (fig. 154, A). These cells are not the result of creasings of the membrane, and they do not disappear when it is stretched. They are usually filled with mucus, which requires to be removed. Over the greater part of the stomach they extend in depth only about $\frac{1}{8}$ or $\frac{1}{6}$th of the thickness of the membrane, but they are larger and deeper near the pylorus. In the ridges between them runs a plexus of vessels larger than ordinary capillaries (fig. 155 A,*d*), and which often retains its blood after death, so as to map out the cells in a beautiful manner. This plexus is supplied by vessels sent up from below, and may be very easily injected artificially.

Fig. 154.



A. Inner surface of the stomach, shewing the cells after the mucus has been washed out. Magnified 25 diameters.

B. Columnar epithelium of the inner surface and cells of the stomach :—*a*. Free ends of the epithelial particles, seen on looking down upon the membrane. *b*. Nuclei visible at a deeper level. *c*. The free ends seen obliquely. *d*. Deep or attached ends of the same. The oval nuclei are seen near the deeper ends.

From the dog. Magnified 300 diameters.

The epithelium which lines these stomach cells and covers the ridges between them is of the columnar variety (fig. 154 B); the particles are shorter than in some other parts: one end is free, while the other is directed towards the basement membrane; and they contain each a clear pellucid nucleus near their deeper end. They seem to lie in a double series, the deeper being in course of developement while the more superficial is in course of decay. It has appeared to us that each particle when arrived at maturity has, besides the nucleus, granular contents enclosed, and that at a subsequent period the granular contents escape at the free extremity by a dehiscence or opening of the wall at that part, leaving the transparent husk with its nucleus subsisting for some time longer. The clear structureless mucus which is almost always found occupying the cells

and covering the surface of the membrane seems to be the altered contents of these particles after their escape, for the uniform existence of a minute cavity in the centre of it, where it fills the cells, shows that it has oozed out from every part of their wall, so as gradually to fill them up (see fig. 155, A).

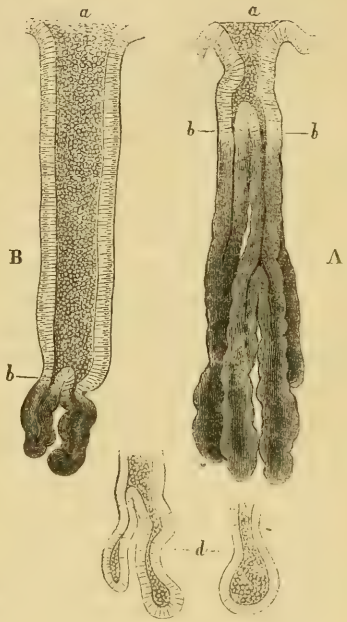
Fig. 155.

A. Horizontal section of a stomach cell, a little way within its orifice. *a.* Basement membrane. *b.* Columnar epithelium. All but the centre of the cavity of the cell is occupied by transparent mucus, which seems to have oozed from the open extremities of the epithelial particles. *c.* Fibrous matrix surrounding and supporting the basement membrane. *d.* Small blood-vessel.

B. Horizontal section of a set of stomach tubes proceeding from a single cell. The letters refer to corresponding parts. The epithelium is glandular; the nuclei very delicate; the cavity of the tubes very small, and in some cases not visible.

From the dog, after twelve hours' fasting. Magnified 200 diameters.

Fig. 156.



Vertical section of a stomach cell, with its tubes: A in the middle region, B in the pyloric region. *a a.* Orifices of the cells on the inner surface of the stomach. *b b.* Different depths at which the columnar epithelium is exchanged for glandular. *c.* Pyloric tube, or prolonged stomach cell. *d.* Pyloric tubes, terminating variously, and lined to their extremities with sub-columnar epithelium.

From the dog, after twelve hours' fasting. Magnified 200 diameters.

It has been said that the cells are so shallow as to dip into the compound membrane only about $\frac{1}{8}$th of its thickness. The rest of its thickness, except near the pylorus, is made up of minute tubular offsets from the bottom of the cells, which may be termed the stomach tubes, (fig. 155, B; and fig. 156,) and which pass vertically, two, three, or four from each cell, afterwards subdividing again and again, and becoming more or less tortuous, till they terminate by blind extremities on a dense tough layer of areolar tissue continuous

with that laxer stratum which separates the mucous from the muscular coat.

The *stomach tubes* have a basement membrane, and contain an epithelium altogether different from that which has been just described. Its particles are of the glandular variety, are rounded in shape, without obvious walls; their contents are darkly granular, often mixed with oil globules, and their nucleus is less distinct. The tubes are so narrow that the particles seem to fill them, and obliterate their cavity, except near their orifices, where they empty themselves into the cells. Towards their blind extremities they often seem to be simply a series or pile of epithelial particles; and this has led some anatomists to deny that they are tubes. The existence, however, of a basement membrane convinces us that they are to be regarded truly as tubes, permanently laid down in the tissue of the stomach, for the origination and discharge of the materials of their peculiar epithelial particles on its inner surface. The tubes proceed in sets, corresponding to the cells into which they open; those of each set being enclosed in a common envelope of nucleated tissue, like the matrix of the kidney and some other glands. This firm investing structure is attached on the one hand to the dense layer on which the compound membrane rests, and on the other to the ridges between the cells; and it sends delicate processes between the individual tubules of each set, and between their branchings, so as to sustain every portion in its proper place. Between the sets of tubules the larger vessels run up to the ridges between the cells, and every tubule is invested with capillaries, which take for the most part an upward direction, and are cut across with the tubules in a transverse section of the latter, (fig. 155, B, *d.*) We have met with no tubular nerve fibres in the mucous membrane of the stomach; but it is highly probable that nucleated nerve fibres run among the tubes, though their want of characteristic features renders it difficult to positively assert their presence.

The description now given will hold good for the whole lining of the stomach, except near the pylorus. Here, in many of the lower animals which we have examined,—for example, in the dog, and, it may with probability be inferred, in man also,—a change occurs in a very gradual manner, but evidently of an important kind. The membrane is of a paler tint, and its cells seem not to terminate at once in the true stomach tubes already described, but are prolonged into much wider cylindrical tubes, lined with the same columnar epithelium, and descending nearly or altogether to the deeper surface of the compound membrane. For the most part, these prolong-

ations of the cells—or, as we shall term them, *pyloric tubes*—end at length in very short and diminutive true stomach tubes (fig. 156, B;) but we have likewise found them terminating in either flask-shaped or undilated extremities, lined throughout with the sub-columnar variety of epithelium, (fig. 156, *d.*) Thus in these animals a marked distinction exists between the mucous membrane of the pyloric compartment and that of the rest of the organ, a distinction which must undoubtedly have an important physiological meaning: and we have suspected that the digestive power of the two parts must differ; that the office of the pyloric tubes resembles that of the stomach cells generally, and is different from that of the true stomach tubes; that perhaps the acid product of the stomach may be furnished by one rather than by the other. We confess, however, that we have been unable, on the one hand, to obtain human stomachs sufficiently fresh and healthy to test the fact of the anatomical distinctness of the two regions in man, or, on the other, to ascertain the value of the conjectures just alluded to as applied to animals in which the twofold structure is sufficiently certain.

It is necessary to examine the changes that occur in the stomach upon the introduction of food in it. These changes are threefold:—1st, as regards its muscular coat; 2nd, as regards its mucous membrane; and, 3rd, with respect to the nature and properties of the secretion which is derived from that membrane.

1. *Movements of the stomach.*—On exposing the stomach of a living animal, or of one recently killed while digestion is going on, we find that it firmly embraces its contents, and that both orifices are closed, so as to prevent the escape of the food. This is particularly the case as regards the pyloric orifice in the first period of digestion. The contraction of the circular muscle which surrounds the pylorus is so strong, that, even after the stomach has been separated from the intestines, its contents do not escape for some time.

This contraction is due to the stimulus of the food; and, when the aliment is difficult of digestion, the muscular coat is proportionably stimulated.

The movements of the stomach are very different in its cardiac and in its pyloric portions. In the cardiac two-thirds the movements are very slow and scarcely perceptible, and seem to consist in little more than a firm and steady contraction upon the contents, the muscular coat thus slowly pushing on the food towards the pyloric portion, and adapting itself to the diminished size of the organ. In the pyloric portion they resemble closely the peristaltic move-

ments of the intestinal canal, which indeed appear, as it were, to start from the junction of this portion of the stomach with its cardiac portion. Under the influence of the magneto-electric apparatus this mode of contraction of the pyloric fibres may be well shewn in dogs or cats just dead, and the contrast with the action of the cardiac fibres may be strikingly displayed.

We had lately an opportunity of observing the peristaltic character of the movement of the pyloric portion of the stomach during life, in a woman in whom that organ was so enormously enlarged as to occupy nearly the entire abdominal cavity, the intestines being pushed into the pelvis, and the arch of the colon lying behind the stomach. The patient was so emaciated, and the abdominal parietes so attenuated, that the action of the viscus could be distinctly seen through them; and it appeared to resemble precisely the vermicular action of the intestines, for which, indeed, it was taken, as the nature of the case could not be distinctly recognized during life.

When the action of the stomach is energetic, a constriction is produced, by which the pyloric third is separated from the cardiac portion, thus giving rise to the hour-glass contraction, which continues for some time after death if the animals have been killed at the moment of its occurrence. The same condition may be produced by the magneto-electric apparatus. This constriction has been noticed by all observers in dogs and cats, and may be now and then seen in the human stomach. In some animals such a division between the two portions of the stomach exists in the natural conformation of the organ.

The muscular action of the stomach in man and the mammalia seems merely to push on the food into the intestine, and not to subject it to any trituration or mechanical reduction, according to the views of the physiologists of the early part of the last century. Reaumur, and after him Spallanzani, introduced into the stomachs of dogs and cats perforated tubes, made some of brittle and others of flexible materials. These were found quite unaltered by the action of the stomach, although the portions of food contained in them were softened and digested.

2. *Changes in the mucous membrane of the stomach.*—The gastric mucous membrane of the stomach of an animal killed during stomach digestion exhibits a faintish red and swollen appearance, due evidently to an increased afflux of blood, excited by the stimulus of the food. In the dog this redness is limited in a very marked manner to the splenic two-thirds, the pyloric third presenting a

white colour and a wrinkled appearance, from the existence of numerous minute folds upon it, which stretching does not obliterate. At the same time the whole surface of the membrane is covered by a layer of mucus, which varies in its thickness and in its viscidity.

It may be inferred from Beaumont's observations, that similar phenomena are met with in the human stomach. Beaumont found, that, immediately on the introduction of food into the stomach, the vessels of the mucous membrane became more injected, much, no doubt, as those of the conjunctiva of the eye would become filled on the application of a foreign body; and that its colour became deeper, being changed from a pale pink to a deep red. A pure, colourless, and slightly viscid fluid, with distinct acid reaction, was then observed to distil from the surface of the membrane, and to collect in drops at various points of it, trickling down the wall of the stomach until it mingled with the food. The exudation of this fluid was always excited by the contact of any foreign substance; even so smooth a substance as the bulb of a thermometer invariably excited it on its introduction, and even when it had been previously ascertained that the stomach was empty, and exhibited no reaction.

During fasting Mr. Beaumont observed no evidence of the existence of such a fluid as this, the sole contents of the stomach being then only a little viscid mucus, occasionally slightly acidulated. Beaumont describes this fluid as being clear, transparent, inodorous, saltish, and resembling in taste thin mucilaginous water slightly acidulated with muriatic acid. It is, he states, readily diffusible in water, wine, or spirits, and effervesces slightly with alkaline carbonates. It coagulates albumen, and is powerfully antiseptic, checking putrefaction in meat. When pure it will keep for many months; but if diluted with saliva, it becomes fœtid in a few days. According to the analysis of Professor Dunglison it contained free muriatic and acetic acids, phosphates and muriates of potass, soda, magnesia, and lime.

Beaumont's observations were made during a period extending between May, 1825, and March, 1833. Various observations and experiments, commencing from a date long antecedent to this, had led to a very generally received opinion among physiologists that the mucous membrane of the stomach was the seat of a special secretion, which had a great share in effecting the changes which the food undergoes in the stomach.

Reaumur was the first to offer satisfactory proof of the secretion of a solvent fluid for the purposes of digestion by the walls of the

stomach. He obtained some of this fluid by making animals swallow sponges, which he could draw out of their stomachs by a string attached; and thus he was enabled to institute experiments on artificial digestion, so as to shew that alimentary substances out of the body could be altered by this fluid in the same manner as they are changed in the stomach. He likewise introduced food into the stomachs of animals in perforated tubes, whereby they were defended from the pressure of the walls of the stomach, but could imbibe its fluids. His experiments disproved the favourite theory of the day, which ascribed all changes of the food in stomach digestion to the influence of trituration upon it by the action of the muscular coat of the stomach: they shewed that the trituration in the gizzard of birds was no more than mastication by teeth in other animals, and that digestion was accomplished in birds of prey, dogs, &c., and probably in man, by the action of a fluid which exerted a solvent influence upon the food.*

Spallanzani likewise illustrated this subject by numerous experiments upon vertebrate animals of all classes, and even upon himself. Following the plan of Reaumur, he obtained the gastric juice by means of sponges, and he introduced food into the stomachs of animals enclosed in perforated tubes and balls. His essay on the subject of digestion is one of the most interesting dissertations in the literature of physiology, and is full of facts proving the secretion of a fluid capable of reducing and dissolving alimentary substances.

Stevens availed himself of a rare opportunity of investigating the effects produced on food in the human stomach. A hussar had accustomed himself at the early age of seven to swallow stones and other hard bodies; and, having continued the practice during twenty years, what had originated in idle amusement was now resorted to as a regular profession, to supply the necessaries of life. When Dr. Stevens first saw him, his stomach was so distended, apparently by the considerable weight to which it was repeatedly exposed, that he could swallow several stones at once, which were not only felt in the stomach, but might be heard by the bystanders moving against each other when the hypogastric region was struck.

Dr. Stevens made this man swallow perforated silver balls, containing sometimes raw animal food, sometimes vegetable substances: in general, raw animal substances suffered less than those which were roasted or boiled ; roasted or boiled animal substances which

* Mém. de l'Acad. des Sciences, an. 1752, pp. 705—752.

had been mechanically divided were most completely acted on; the substances contained in balls with large holes were more completely acted on than those contained in balls with minute holes; and, lastly, the various vegetable grains, as wheat, rye, barley, oats, and peas, were least of all altered, having only become moistened and swollen, while bone underwent no change.

Dr. Stevens also introduced leeches and earthworms in his perforated spheres, and found that even these animals, though introduced living, were dissolved as inanimate matters.*

John Hunter made some observations which furnished an interesting proof of the existence of a solvent gastric fluid. He was struck with the condition of the stomach in two cases of sudden and violent death. A man had his skull fractured by a single blow of a poker: just before the accident he was in perfect health, and had taken a hearty supper. Upon opening the abdomen, he found that the stomach, though it still contained a good deal, was dissolved at its great end, and a considerable part of its contents lay loose in the general cavity of the belly; a circumstance, he adds, which puzzled him very much. The second instance was in a man who died at St. George's Hospital a few hours after receiving a blow on his head which fractured his skull. In both these cases the solution was at the splenic end of the stomach; the edges of the opening and the mucous membrane for some distance within were half dissolved, "very much," says Hunter, "like that kind of digestion which fleshy parts undergo when half digested in a living stomach, or when acted upon by a caustic alkali, viz. pulpy, tender, ragged."

"In these cases," Mr. Hunter adds, "the contents of the stomach are generally found loose in the cavity of the abdomen about the spleen and diaphragm; and in many subjects the influence of this digestive power extends much farther than through the stomach. I have often found, that, after the stomach had been dissolved at the usual place, its contents let loose had come into contact with the spleen and diaphragm, had dissolved the diaphragm quite through, and had partly affected the adjacent side of the spleen; so that what had been contained in the stomach was found in the cavity of the thorax, and had even affected the lungs to a small degree."

"There are very few dead bodies in which the stomach at its great-end is not in some degree digested; and one who is acquainted with dissection can easily trace these gradations. To be sensible of

* De Alimentorum Concoctione, Edin. 1777, (in Smellie's Thes. Med.)

this effect, nothing more is necessary than to compare the inner surface of the great end of the stomach with any other part of its inner surface: the sound portions will appear soft, spongy, and granulated, and without distinct blood-vessels, opake and thick; while the others will appear smooth, thin, and more transparent, and the vessels will be seen ramifying in its substance; and upon squeezing the blood which they contain from the larger branches to the smaller it will be found to pass out at the digested ends of the vessels, and to appear like drops on the inner surface."*

Hunter remarked that solution of the stomach is very commonly found in fishes, which almost always die a violent death, and frequently during digestion.†

Dr. Carswell investigated this subject, and obtained results confirmatory of the views of John Hunter. He killed rabbits and dogs during the digestive process, allowing them to lie for various periods after death. If examined four hours after death, he found that the solution had affected the mucous, submucous, and muscular tunics: when six hours had elapsed, the peritoneal coat was found softened, in addition to the others; the stomach was consequently perforated, and the food passed through the opening and came in contact with the liver, spleen, diaphragm, and intestines, one or all of which exhibited the same kind of softening as that found in the stomach, at those places where the digested food touched the parts. In another series of experiments, where the animals were suffered to lie for a still longer period after being killed, perforation of the diaphragm or œsophagus had taken place, and the liquid part of the food had flowed into the cavity of the chest, causing digestion and softening of the pleura and of the lungs.‡

3. *The gastric juice.*—From these various sources we derive the most ample evidence of the existence of a fluid secreted by the walls of the stomach during digestion, capable of exerting a reducing or solvent influence upon food. This fluid is the *gastric juice* —the *succus gastricus.*

It is of great importance to a correct theory of digestion to determine the precise composition of this fluid. Dr. Prout, in this country, in 1823, two years prior to the commencement of Beaumont's experiments, had determined the existence of an acid fluid secreted during digestion, and had analysed it in the rabbit, hare,

* Hunter's Animal Œconomy, Owen's edition, p. 119.

† Spallanzani confirmed Hunter's statements.

‡ Ed. Med. and Surg. Journal, vol. xxxiv. p. 262. See also an excellent delineation of this post mortem condition by Dr. Carswell, in his "Illustrations of the Elementary Forms of Disease," art. *Softening.*

horse, calf, and dog. And he announced, as the result of his analyses, "that free or at least unsaturated muriatic acid in no small quantity exists in the stomach of those animals during the digestive process." And in later publications Dr. Prout has reasserted this statement.

The weight which is so deservedly attached to the opinion of this eminent philosopher has, no doubt, had great influence in determining the prevalent opinion in this country in favour of the view which attributes the acidity of the gastric fluid to the existence of free muriatic acid in it. The source of the acid, it is generally believed, is the chloride of sodium of the blood, which at the mucous membrane of the stomach contributes muriatic or hydrochloric acid to the gastric juice, leaving free soda to be carried to the liver by the veins of the stomach.

Experiment, however, shows that muriatic acid has little or no solvent power on the food, and that the reducing action of the gastric fluid cannot be attributed to it alone. Albumen or meat subjected to the action of water acidulated with muriatic acid, and kept for some hours at a temperature of 100°, undergoes no change of any importance: neither substance exhibits any softening or tendency to putrefaction or decomposition of any kind. Similar experiments with acetic acid or with phosphoric acid lead to like results.

It is plain, then, that, the solvent powers of the gastric fluid are not due simply to the acid which it contains, whatever that may be, and that we must look for some other ingredient in it, which, either alone or in combination with acid, can exercise these powers. The clue to this was given by Eberle, who adopted the expedient of adding to water acidulated with muriatic acid a small piece of the mucous membrane of the stomach. By this means he succeeded in obtaining a digestive fluid which reduced animal substances as perfectly as the gastric juice itself.

This discovery was of the last importance to the formation of a correct theory of stomach digestion, and to exact views of the nature of the gastric juice. It was soon followed up by numerous experiments in Germany by Schwann and Müller, and by Purkinje and Pappenheim. The general result of these experiments was, that the addition of a portion of gastric mucous membrane from the true secreting stomach to an acidulated water produced a perfect digestive fluid; but that no other mucous membrane would answer this purpose. The following changes take place on macerating meat and albumen in a digestive fluid:—The meat is broken down to a complete pulp; and, if the digestion have been con-

tinued sufficiently long, it is dissolved. The albumen is likewise equally softened. The early changes which take place in a cubic piece of solid white of egg, macerated in the digestive fluid, are very characteristic. Its edges become of a pearly hue, semi-transparent, almost fluid, breaking down under the slightest touch of the finger ; and, after longer digestion, the solid matters are completely dissolved.

The solvent power of a digestive fluid made with the mucous membrane of the stomach is strikingly displayed if the results of the digestion of meat and albumen with it be compared with those obtained by digesting pieces of the same substances either with simply acidulated water,—muriatic, acetic, or phosphoric acids, being used,—or with an infusion of mucous membrane without acid. Simple acidulated fluids produce little or no change in meat and albumen in the course of twelve or twenty-four hours ; and such change as is produced presents a marked contrast to that caused by the infusion of mucous membrane with acid. No acid, however, appears to cause more change than the phosphoric. When the infusion of mucous membrane is used *without* acid, rapid putrescence is produced. A similar effect results, although with less intensity, from the use of too little acid ; and, if alkali be added, the putrefaction becomes still more rapid and intense.

In these experiments, it is of great importance to pay close attention to the temperature. It should be within the range of from 90° to 110°, the higher temperature increasing the energy of the digestive action. If it reach the point at which albumen is coagulated, all solvent change ceases, and the meat or albumen becomes hardened. In a low temperature, likewise, there is no change ; the digestive fluid under such circumstances serving merely to prevent decomposition.

The *antiseptic power* of an acid infusion of gastric mucous membrane is one of its most remarkable properties; and in this respect it resembles the gastric fluid itself, which, according to all observers, is remarkably antiseptic, being capable of checking the further progress of putrefaction in meat in which that process had already begun. This power seems principally due to the acid, the neutralization of which destroys it; and, if an infusion of mucous membrane to which enough acid had not been added become putrescent, its further decomposition may be checked by the addition of more acid. We have kept the artificial digestive fluid for many months in a bottle with a common cork without its undergoing any change.

The gastric fluid possesses the property of causing the coagulation of the caseine of milk; an artificial digestive fluid made from the mucous membrane of the true stomach of ruminants possesses the same power, even if its acid be neutralized by potass. This fact has been long known to the makers of cheese; and the dried mucous membrane of the fourth stomach of the calf has been used, under the name of rennet, for the purpose of coagulating that principle in milk. That it possesses this power independently of any acid which it may contain, was first pointed out by Berzelius. Some have affirmed that this power belongs only to the mucous membrane of the stomach of sucking animals.

A fluid of such digestive power as that above described cannot be made from any mucous membrane but that of the stomach. The mucous membrane of the bladder, of the greatest portion of the intestinal canal, is quite insufficient for this purpose; but that of the duodenum appears to exert some solvent influence.

The organic principle of the Gastric Juice.—All these facts show that the gastric mucous membrane contains some material, which, when dissolved or diffused in acidulated water, exercises a power not to be distinguished from that of the gastric juice itself. Can this material be isolated? There is no doubt that we can obtain from the mucous membrane of the digestive stomach of animals, an organic substance, which exhibits reactions in close analogy with those of albumen, and which exercises a solvent or catalytic influence upon various azotised substances; to this substance Schwann and Müller gave the name "*pepsine*."*

Valentin very justly remarks that the organic combinations upon which the solvent power of the gastric fluid depends, share the same fate with other contact substances, namely, that they cannot be obtained in perfect purity, nor can their precise relative proportions be determined with exactness. Pepsine, therefore, he adds, can only be regarded as a hypothetical or conventional name for an unknown mass which may be separated by alcohol, or by lead and alcohol in combination with other bodies. Nor do the reagents indicate any definite character—they only afford conjectural information. To view it as a kind of diastase, whilst it does not remove our difficulty, nevertheless denotes the power of the unknown substance in a more precise and definite manner.

An artificial digestive fluid may be made in the following manner. Let a piece of the mucous membrane of the stomach of a pig be macerated in distilled water for twelve hours at the temperature

* Also called *gasterase* by French writers.

of 98° or 100°; afterwards add dilute muriatic acid to the fluid until it redissolves the precipitate which is at first thrown down; the fluid thus formed will be found to possess full digestive powers, and all the properties of the gastric fluid. It is, in fact, an acidulated solution of pepsine in water. The pepsine may be precipitated from this solution by some of the reagents which coagulate albumen. Bichloride of mercury will do this, and render the fluid inert. Alcohol and water at the boiling temperature produce the same effect: the precipitate, however, thrown down by alcohol, is capable of being redissolved in water, and then, with acid, will produce a digestive fluid. Tannin also precipitates it. It is evident, therefore, that the digestive fluid contains a principle capable of affording distinct reactions. The solvents of this principle are water and dilute muriatic or acetic acids.

The power which the digestive fluid has of coagulating caseine, *independently of its acid*, denotes that it holds in solution some special agent derived from the mucous membrane of the stomach.

Alcohol added to a fresh infusion of mucous membrane throws down a white flocculent precipitate, which may be collected on a filter, and when dried will produce a grey compact mass. This, when redissolved in water, will exhibit digestive powers, and these powers are greatest when it is united with acetic and muriatic acids. We obtain in this way the nearest approach to the isolation of pepsine.

The acid of the Gastric Juice.—Of the existence of an organic principle, a secondary organic compound, the product of the secretory action of the mucous membrane of the stomach, no doubt can be entertained; but we can speak with less certainty of the nature of the acid which exists along with it in the gastric fluid of the stomach, inasmuch as recent observers have thrown a doubt upon the correctness of Prout's opinion. The following are the most recent opinions put forward on this subject.

Blondlot affirms that the acidity of the gastric juice is due not to the presence of a free acid, but to the existence of *biphosphate of lime* as one of its ingredients. To this, however, Melsens and Dumas raise the objection that carbonate of lime, or Iceland spar, placed in gastric juice for some hours becomes corroded and suffers a very notable diminution of weight, which can arise solely from the presence of a free acid. MM. Bernard and Barreswil likewise state some strong objections to the views of M. Blondlot in a paper published in 1844. They show that M. Blondlot failed to obtain effervescence by adding carbonate of lime to gastric juice,

because he employed a too much diluted fluid: on concentrating the gastric juice a little the effect was readily produced. Admitting that a free acid is present, they deny that it is hydrochloric acid, because that acid exists in the gastric fluid only in the state of chloride. If a minute quantity of oxalic acid be added to the gastric juice, a precipitation is occasioned by the formation of insoluble oxalate of lime; whilst an equal quantity of the same reagent, added to distilled water containing a two-thousandth part of hydrochloric acid, to which chloride of lime had been added, produced no such effect. The lime of the gastric juice unites with the oxalic acid; but that acid will not displace lime from its connexion with hydrochloric acid. Nor is the acid of the gastric juice free acetic acid; the most delicate tests failed to detect it. MM. Bernard and Barreswil infer that there is in the gastric fluid a minute proportion of phosphoric acid, which, however, is not the only free acid. The lactic acid, according to these observers, is the principal acid of the gastric juice, because the behaviour of a fluid acidulated with that acid corresponds very exactly under chemical examination with that of the gastric juice. Thus the distillation of water acidulated with lactic acid exhibits exactly the same stages as that of the gastric fluid,—first, there passes over only pure water, in the next stage an acid liquid, in which salts of silver do not throw down a precipitate, and there remains a strongly acid fluid effervescing with carbonates; in this remaining liquid hydrochloric acid may be detected if a minute quantity of chloride of sodium had been added to the fluid previous to distillation.

The acid of the gastric juice produces salts of zinc, lime, baryta, and copper, similar to those formed by lactic acid; and MM. Bernard and Barreswil affirm that it readily decomposes the chlorides in concentrated solutions. Hence it is that hydrochloric acid passes over in the last products of the distillation of the gastric juice.

These authors also state that the nature of the food appears to exercise no influence upon the nature of the acid, and that they have always found free lactic acid, whether after an exclusive vegetable or animal regimen continued for many days, or after a prolonged very sparing diet.

Dr. R. D. Thomson, of Glasgow, in a paper published in 1845, also disproves the opinion of Blondlot by experiment, and comes to the conclusion that the free acid of the stomach, in the digestion of vegetable matter at least, of all the known acids corresponds only with the lactic.

Lehmann attributes the acidity of the gastric fluid to both free hydrochloric and lactic acids. He obtained the former from the stomach of a diabetic patient, to whom he had administered an ipecacuanha emetic; and the latter from the stomach of a cat, from which he was able to procure distinct crystals of lactate of zinc. In subsequent researches Lehmann confirmed this conclusion respecting the nature of the acid of the gastric fluid.

Liebig lends his sanction to this doctrine, and especially to the view put forward by Bernard and Barreswil, that both lactic and phosphoric acids exist in this fluid free, while there is no reason to deny the existence of an acid phosphate likewise. The opinion that free lactic acid exists in the gastric fluid is not new. It was put forward by Chevreul many years ago, and afterwards by Leuret and Lassaigne. In 1823 our distinguished friend, Dr. Graves, of Dublin, published analyses of the fluid of the stomach from two patients, in which he found free lactic acid in abundance. Notwithstanding what has been done on this subject it must be confessed that the full truth has scarcely yet been arrived at. We have yet to learn whether the constitution of the gastric juice is constant—whether the same acids or acidifying agents are present in all animals, and under all conditions of feeding and food; and we have also to ascertain whether any and what changes may be produced by disease in the chemical characters of the gastric fluid. The inquiry, taken up on a large scale among the lower animals, and extended to man, in health and disease, would, no doubt, yield most valuable and interesting results.

The digestive principle does not seem to be secreted in equal quantity or of equal power at all parts of the stomach. Meat and albumen, digested with mucous membrane from the cardia, is by no means so much acted upon as if digested with mucous membrane from the pylorus or from the central part of the stomach. In the pig there is a large patch of the membrane of a reddish hue, and of considerable thickness, forming that portion of the mucous membrane which corresponds to the middle of the great curvature of the stomach; this, we find, exercises a more energetic action upon meat or albumen than any other part.

It is highly interesting to notice that the mucus which accumulates upon the surface of the mucous membrane of the stomach has a digesting power corresponding to that of the portion of mucous membrane from which it has been taken. This we have determined by our own experiments.

Nature of the digesting power of the Gastric Juice.—Having

stated the leading facts which observation and experiment have developed respecting the act of digestion in the stomach, it remains to inquire what is the real nature of the digesting power of the gastric fluid.

Two questions present themselves for consideration: is the digesting power of the stomach a true solvent power, producing simply a *solution* of the matters submitted to its action, without effecting any change in their chemical constitution? or does the digestive fluid exercise a catalytic action on the substances submitted to it, whereby it effects a *chemical decomposition* of them, similar to that produced in barley by diastase, whereby the starch of the grain is converted into sugar, or like the action of yeast upon sugar, whereby the latter is decomposed into carbonic acid and alcohol?

To decide these questions, it is necessary to examine the exact nature of the changes produced in the food by stomach digestion.

Milk.—If milk be introduced into the stomach, its caseine is first coagulated and afterwards apparently dissolved. The solidified caseine seems gradually to melt down and becomes absorbed. In overfed infants milk-curd appears in the stools in considerable quantity, the child having received so much milk that its stomach is unable to digest the caseine precipitated from it. When, however, the quantity of milk is in just proportion to the digestive power of the stomach, all the curd is digested, and therefore none is found in the stools.

Albumen.—White of egg (ovalbumen), if swallowed raw, is immediately coagulated by the gastric juice and then dissolved. Tiedemann and Gmelin found that after three hours sojourn in the stomach of a dog albumen was dissolved, forming "a yellowish mucous liquor," which coagulated readily by heat.

Coagulated albumen becomes softened down and dissolved in the fluids of the stomach, from which it may again be precipitated by heat or nitric acid.

In experiments with the artificial digestive fluid, we find that if the fluid in which albumen had been digested be carefully filtered and subjected to heat and nitric acid, a copious precipitate of albumen will take place.

Meat is softened, gelatinized, and dissolved, and albumen may be precipitated by heat, nitric acid, or ferro-cyanate of potass from the liquids obtained from the stomach.

Vegetable Substances.—In all the experiments upon animals of the carnivorous kind (cats, dogs), bread, potatoes, and other vegetable substances underwent change much more slowly than animal

matters, and they became softened by admixture with the fluids of the stomach and appeared partially dissolved.

Boiled starch, in Tiedemann and Gmelin's experiments, underwent solution, and then did not exhibit its characteristic blue colour with iodine. In a dog, killed five hours after a meal of boiled starch, the contents of the stomach underwent no change of colour with iodine, but appeared charged with sugar and with a kind of gum of starch (*dextrine*). In another dog, similarly fed, and killed three hours afterwards, the starch which was dissolved did not react in the usual manner with iodine, but some portions not yet dissolved did exhibit the characteristic reactions. It would seem that immediately the starch becomes dissolved by the gastric fluid it loses its characteristic property of forming the blue iodide of starch.*

In the artificial digestion of starch, with the mucous membrane of the human stomach, we have not succeeded in producing any change in the starch: it still evinced its usual reaction with the iodine test. We have, however, found that starch digested for some time in this way evolved a peculiar sour smell like that of cheese.

Bouchardat and Sandras report, respecting the influence of stomach-digestion upon starch and upon amylaceous elements, differently from Tiedemann and Gmelin. They state that they have been unable to obtain any evidence of the conversion of starch into sugar; that neither by fermentation, nor by the polarizing apparatus of M. Biot, have they succeeded in procuring any indication of the existence of sugar in the digested substances; and they were equally unsuccessful in detecting the formation of dextrine. Lactic acid, however, appeared to them to be formed in much larger quantity after a meal of starch than after one of fibrine or of gluten. These observers likewise state as the result of their experiments, that in the human subject and in the carnivora feculent substances are digested with extreme slowness, and not at all unless the integument of the starch grain have been ruptured by boiling.

Fatty or oily substances, as suet, fat, oil, butter, or wax, undergo no change in the stomach, according to Bouchardat and Sandras, after the lapse of some hours, and may be found in that organ unchanged in the midst of other matters upon which the stomach exercises a solvent action.

This we have observed in our own experiments; and on perusing the MS. notes of the results of various experiments made thirty

* Tiedemann and Gmelin, Recherches sur la Digestion, par Jourdain, t. i. p. 340.

years ago by Sir B. C. Brodie, and with great kindness placed at our disposal by him, we find the following statement: "when dogs were fed on lard, the lard passed into the small intestine unchanged."

It would seem to be the most reasonable conclusion which we can deduce from the preceding statements, that in man and the carnivora the fluid secreted by the stomach during digestion simply dissolves animal and vegetable substances of the azotized kind, without altering their chemical constitution, leaving amylaceous, oily, saccharine, and the allied substances but little or not at all acted upon.

The Chyme.—The mass that is contained in the stomach after digestion has been going on for four or five hours, and which is commonly known by the name of *chyme*, consists of aliments dissolved, or softened and prepared for solution or other change by the gastric juice. As they are mostly of the same kind, this mass presents a homogeneous appearance, except when substances are present which either require a longer sojourn in the stomach or are only digestible by some lower portion of the intestinal tube.

Rate of Stomach Digestion.—The process of stomach digestion is a slow one. In the artificial digestions above referred to, it took from eight to twelve hours to produce any marked effect upon the pieces of meat and albumen submitted to the action of the digestive fluid. This, however, is much longer than the natural process. According to Dr. Beaumont's researches upon Alexis St. Martin, it took three or four hours before the stomach became empty after a meal, consisting chiefly of azotized food—and his tables show that the mean time required for the digestion of the principal animal substances in common use, such as butcher's meat, fowl, game, was from two hours and three-quarters to four hours.

In experiments on dogs, it has been found by most experimenters that no great advance in the solution of the contents of the stomach is made under from two to four hours. Gosse, who possessed the power of disgorging the contents of his stomach by previously swallowing a quantity of air, found that no change had taken place in the food after it had remained half an hour in the stomach: after the lapse of an hour he found the food much softened—but not reduced in weight: while, after two hours, it was not only much softened but considerably reduced in quantity, so that he could not return from his stomach more than half what he had taken.*

Purkinje and Pappenheim found, in their experiments upon arti-

* Œuvres de Spallanzani, par Senebier, t. ii.

ficial digestion, that, by gently shaking the tubes in which the process of digestion was going on, it became accelerated. This accords with what daily experience points out to us, namely, that agreeable and lively conversation during a meal, or gentle exercise after one, invariably promotes the primary stages of digestion.

Violent exercise after meals retards digestion, most probably by preventing the constant action of the gastric fluid upon the pieces of food in it—the movements of the body causing frequent change of place in the morsels of food.

The use of alcoholic stimulants also retards digestion, by coagulating the pepsine, and thereby interfering with its action. Were it not that wine and spirits are rapidly absorbed, the introduction of them into the stomach in any quantity would be a complete bar to the solution of the food, as the pepsine would be precipitated from solution as quickly as it was secreted by the stomach.

Absorption by the Stomach.— An important question, to which as yet we can give no certain reply, is as to what becomes of the food after it has been duly dissolved by the fluids of the stomach. When we find how completely albuminous and fibrinous substances are dissolved by digestion in the natural or artificial gastric fluid, it cannot be doubted that they are in a state fit for absorption while yet in the stomach, nor can there be any good reason to deny that a considerable quantity must be absorbed without passing further on in the alimentary canal. The great rapidity with which liquids of a simple and limpid kind, or the aqueous solutions of certain salts, as iodide of potassium, the alkaline carbonates, &c., find their way into the blood, denotes that this must take place very quickly after they have been swallowed, and that the bloodvessels of the stomach must be the principal channel through which they effect their entrance into the circulating system, and it scarcely admits of doubt that the dissolved aliments are removed through the same channels.*

The venous blood of the stomach passes to the vena portæ. Hence, matters absorbed by the sanguiferous system of the stomach pass by a very direct route to the liver, and probably excite that gland to increased secretion for the purposes of digestion in the small intestine.

The gastric fluid dissolves perfectly only the fibrinous and albuminous animal substances, and probably also the glutinous or azotised portion of vegetable food; we must suppose, therefore, that it is only

* We have detected iodine in the saliva and urine in twenty minutes after a solution of a few grains of iodide of potassium in a large quantity of water had been swallowed.

these portions of the solid aliments which are absorbed by the stomach. Drinks, as water and various other liquids, fermented or not, are, doubtless, likewise in great part absorbed in the same way. All other kinds of food, and such remaining portions of the azotised or liquid aliments as have escaped absorption by the stomach, after having undergone to a certain extent maceration in it, are pushed onwards into other parts of the digestive tube there to undergo further changes to fit them for being absorbed.

Eructation and Vomiting.—As there can be no doubt that the movements of the stomach are capable of pushing on the food towards the intestinal canal, it appears *primâ facie* extremely probable that the same muscular force may cause it to evacuate its contents through the œsophagus, if there be any obstacle to their downward passage, too strong to be overcome.* The muscular coat of the stomach, pressing by its passive contraction upon its contents, will cause them to pass in that direction which offers the least resistance. Now, in a state of health, the food, in order to return by the œsophagus must not only overcome the passive contraction of the muscular coat of that tube, but it must also ascend against gravity. Moreover, the action of the fibres of the splenic extremity of the stomach favours the passage of the food toward the pylorus. Hence, not only is there least resistance at the pylorus, but there is likewise a *vis a tergo*, which favours the propulsion of the food in that direction.

When, however, air accumulates at the cardia in such quantity as to distend that portion of the stomach, it opens the œsophagus by its expansile force, and from its lightness rushes up the œsophagus, carrying with it sometimes liquid or solid food. When air is generated in large quantity and with great rapidity, it is wonderful how much may escape in this way, and large quantities of food may be discharged from the stomach at the same time, solely by the convective force of the large bubbles of air ascending from it. This is *eructation*—it seems due solely to the presence of a large quantity of air in the stomach.

Vomiting is an act of a more complex character than eructation; by it solids and liquids may be expelled from the stomach through the œsophagus, even contrary to gravity. We must assume that a necessary condition for the production of the act of vomiting is the existence of obstruction at or near the pyloric portion of the

* The old and still prevalent notion of an inversion in the action of the stomach is most probably erroneous. The inversion is only apparent, not real. See an able paper by Dr. Brinton on this subject.—Lond. Med. Gazette, 1849.

stomach, which prevents or opposes the passage of the gastric contents in that direction. Probably the whole of the pyloric third of the stomach is strongly contracted under the circumstances which ordinarily give rise to vomiting; and the contents of the viscus having been accumulated in its cardiac two-thirds, are thus brought into more immediate and direct communication with the œsophagus. The pylorus being closed against them, the stomach contents are forced through the œsophagus, not only by the muscular contraction of the stomach itself, but also by that of the abdominal muscles and the diaphragm.*

It is probable that where a very complete obstruction exists at or near the pylorus, as in cases of hernia and other mechanical obstacles, the act of vomiting partakes much of the nature of an overflow, and requires no more than the action of the muscular coat of the stomach itself. The slight effort which accompanies the discharge of the stomach's contents in cases of this description, denotes this. But when vomiting is caused by an emetic, or is the result of sea-sickness, or of nervous irritation, as in stimulation of the fauces, or in brain disease, an active, and almost convulsive, contraction of the diaphragm and abdominal muscles accompanies it, and, no doubt, constitutes the principal expelling force. These muscles by their simultaneous forcible contraction form two plane surfaces, one passing downwards and backwards, the other nearly vertically downwards, which are approximated very closely to each other, and compressing the stomach between them, cause the forcible ejection of its contents in that direction, which offers least or no resistance, namely, through the œsophagus.

The act of vomiting is ushered in by a deep inspiration, during which the diaphragm is firmly contracted. Just at this moment the abdominal muscles contract forcibly and almost convulsively. Thus an effort at expiration, in which, doubtless, other muscles take part, besides those of the abdominal walls, quickly succeeds the act of inspiration. But the diaphragm does not become relaxed as in ordinary expiratory efforts, because the air is only very partially and slowly expelled. For, at the same time that the abdominal muscles and the diaphragm are thrown into contraction, those of the glottis are exerted to a like convulsive action, and maintain a partially closed state of the glottis which resists the ex-

* The power of returning portions of the food at will (*rumination*), which some men have acquired, is effected by a strong voluntary contraction of the pyloric muscle, and by expulsive efforts operating directly on the cardia portion of the stomach, which can thus expel its contents only in the upward direction.

pulsion of air from the lungs and keeps them in a certain state of distension until the effort of vomiting is over, when the diaphragm relaxes and complete expiration takes place. That there cannot be complete closure of the glottis in the effort of vomiting is shown by the fact that that act is very frequently accompanied by a loud explosive noise which must be formed in an open, although a resisting glottis.

Dr. Anderson has shown by direct experiment that when dogs vomit under the influence of tartar emetic, the diaphragm is forcibly contracted. He introduced his finger into the abdomen, and found that during each effort of vomiting the diaphragm became tense and rigid, and descended towards the abdomen. And this he found took place even when the trachea had been previously opened, whence we may infer that the force of the expiratory muscles is spent chiefly upon the stomach.*

A warm controversy took place in the last century, and was revived in the present, with reference to the share which the stomach itself takes in the act of vomiting. Many high names in physiology took part in this discussion, some maintaining, among whom was John Hunter, and, subsequently, Majendie, that the stomach was perfectly passive, and that the abdominal muscles and the diaphragm were the sole agents of expulsion, while others, as Haller, Rudolphi, &c., allowed that the contractions of these muscles only assist the expulsive efforts of the stomach, which, in some instances, may act independently of the surrounding muscles. Maingault affirmed that he had seen vomiting occur after the division of the diaphragm and the abdominal muscles, and Rudolphi made the same assertion. And the Committee of the French Academy appointed to investigate the question, admitted that it needed only a very slight external pressure to produce vomiting, and that distinct contractions of the muscular coat of the stomach were seen during the act in the neighbourhood of the pylorus. The question is one which cannot be decided by cruel experiments, unless it can be shown in several instances that vomiting can take place under conditions which render the abdominal muscles and diaphragm incapable of acting; such evidence would unequivocally demonstrate the activity of the stomach.† But the opposite experiments, such as the non-

* See Anderson, Lond. and Edin. Monthly Journal, 1844. In this paper Dr. Anderson has given a complete refutation of Dr. Marshall Hall's supposition that the diaphragm is inactive in vomiting.

† M. L'Epione records, in the Bulletin de l'Académie de Médecine, a case in point. A man's abdomen was torn open by a horn, and the stomach wholly pro-

occurrence of vomiting when the abdominal muscles and diaphragm have been paralysed, or its occurrence when an inert bag, as a pig's bladder, has been substituted for the stomach, the external muscles being intact (as in Majendie's noted but most cruel experiment), lead to no conclusion, for, in the one case the violence done so impairs the conditions necessary for the act (both nervous and muscular) that it cannot be expected to take place; and in the other, the substitution of the inert bag, and the section of the œsophagus, are favourable to the escape of fluids from the former and through the latter, under the slightest pressure.

The nervous changes which take place in the act of vomiting are of the most interesting kind. It must be borne in mind that this act may take place—1st. from the introduction of certain substances into the stomach, some of which, as bile, mustard, common salt, not becoming absorbed, must act simply by the impression they make on the mucous membrane; 2. by the introduction of emetics, as Tartar emetic, into the blood, or by the presence of certain morbid poisons in that fluid; 3. by mental emotion, as that excited by the sight of a disgusting object; 4. by irritation at the base of the brain. Vomiting may be caused, therefore, either by the direct application of a stimulus to the gastric surface, or by the disturbance of some part of the brain through the presence of particular substances in the blood, that is, by causes operating from periphery to centre, or by causes acting directly on the centre itself. Either the disturbing cause, as tartar emetic in the blood, affects the medulla oblongata, in which are implanted the vagi nerves; or some of the fibres of these nerves propagate to the centre the effects of the peripheral irritation at the gastric mucous membrane. When the medulla oblongata is thrown into excitement by any of the causes abovementioned, certain motor nerves implanted in it, are stimulated to action, and the abdominal muscles, the diaphragm, and the muscles of the larynx as well as the muscular fibres of the stomach and œsophagus, are thrown into that combined action which is essential to the production of active vomiting.

When vomiting is the result of a peripheral stimulation, it affords a remarkable example of a reflex or physical nervous action of the most complex kind, in which, from the excitation of a few sentient nerves, the nervous force is made to radiate upon several

truded. For half an hour it was seen repeatedly and forcibly contracting itself, till by its own efforts it expelled all its contents except the gases.—See Paget's Report for 1845.

muscles and to excite to simultaneous and combined action some which usually antagonise each other, and are, therefore, never, excepting in this act, in the same condition at the same time. We allude to the abdominal muscles and the diaphragm; the former as muscles of expiration being the habitual antagonists of the latter, which is the great muscle of inspiration. In short, the excitation of the nervous centre, which is sufficient to cause vomiting, gives rise to a forcible act of respiration, in which the act of expiration is so powerfully opposed by the contracted state of the constrictors of the larynx, the diaphragm also remaining in strong contraction, that the main force of the expiratory muscles is directed to compress the stomach against the latter muscle.*

* On the subjects of this chapter see the various works on Anatomy, and the principal systems of Physiology previously referred to; Œuvres de Spallanzani; Tiedemann et Gmelin sur la Digestion; Hunter's Animal Œconomy, by Owen; Eberle, Physiologie der Verdauung, 1834; Simon's Chemistry, by Day; Dumas, Traité de Chimie, tom. viii. (1846); Beaumont on Digestion; Blondlot sur la Digestion; Dr. Kirkes' excellent Manual of Physiology; Bouchardat and Sandras, Comptes Rendus for 1844; Bernard and Barreswil, Comptes Rendus, 1844; Dr. R. D. Thomson, Lond. Med. Gaz. 1845.

CHAPTER XXV.

OF INTESTINAL DIGESTION. — ANATOMY OF THE INTESTINAL CANAL IN MAN AND VERTEBRATA. — THE MUCOUS MEMBRANE OF THE INTESTINE. — ITS FOLDS AND VILLI. — ITS GLANDS. — DIGESTION IN THE SMALL INTESTINE. — FLUIDS POURED INTO THE SMALL INTESTINE. — THE PANCREATIC FLUID. — THE BILE. — THEIR INFLUENCE. — DIGESTION IN THE LARGE INTESTINE. — DEFÆCATION.

Anatomy of the Intestinal Canal.—The intestinal canal commences at the pylorus and terminates at the anus. It exhibits a very obvious subdivision into two portions: a narrower and much longer portion, disposed in numerous coils or convolutions, which is called *the small intestine* (intestinum tenue); and a much wider but shorter portion, *the large intestine* (intestinum crassum). The length of the whole intestinal canal in the adult is between thirty and forty feet, or about six times that of the body: the small intestine forms five-sixths of this.

There is a very distinct natural demarcation between these two portions of the intestinal canal; the large intestine commences by a dilated cul-de-sac, which communicates on its inner side with the small intestine. This portion, which is the widest part of the large intestine, is lodged in the right iliac fossa; it constitutes the commencement or the head of the colon, and as it forms a blind extremity or cul de sac beyond the junction of the small intestine with it, it is named *caput cæcum coli*, or commonly *cæcum*. Connected with it is a remarkable appendix, which proceeds from its inner and posterior part, and hangs down into the pelvis in a slightly curved form, which gives it the appearance of a worm (lumbricus), and receiving support from a small fold of peritoneum. This is called the *appendix cæci vermiformis*. It is a small process from the cæcum, hollow, cylindrical, in size rather larger than a goose-quill, about three inches long, and ending in a blind extremity which lies free in the pelvis, but having a free communication with the cæcum where it is attached to that intestine. The large intestine commencing at this part ascends from the right iliac fossa, through the right lumbar region, as high as the concave surface of the liver;

this forms the *right* or *ascending colon;* at the liver it turns to the left, and passes, in an arched form, across the abdomen from the right to the left hypochondrium, thus forming *the transverse colon,* or *the arch of the colon;* it then turns downward, passes through the left lumbar region to the left iliac fossa; this portion, which is straight or nearly so, is the *left* or *descending colon.* In the left iliac fossa the intestine becomes somewhat curved, and is rather loosely attached to the wall of the pelvis; its curve resembles the letter S; this portion terminates in the pelvis, and is named *the sigmoid flexure of the colon;* lastly, this becomes continuous with the pelvic or terminal portion of the intestine, which, although far from being straight, is designated *intestinum rectum* or commonly *the rectum.* This opens externally at the *anus*, its mucous membrane becoming continuous with the skin at that orifice.

The small intestine is arranged in many convolutions, and, with the exception of its upper portion, *the duodenum*, it is quite loose in the cavity of the abdomen and even in that of the pelvis, occupying the central part of those cavities. The large intestine or colon embraces it on the right, above, and on the left. Three portions of the small intestine have always been recognised by anatomists, which, although not distinguished by any well-marked external boundaries, exhibit in their mucous membrane features (to be pointed out hereafter) which form their most appropriate means of distinction. The upper portion is sufficiently distinct from the rest by its dilated form, its horse-shoe curve, and by being closely fixed to the spine, in the greatest part of its extent, by peritoneum. This is *the duodenum:* it forms about the first twelve inches of the small intestine.

The middle portion of the small intestine is the *jejunum*, and the terminal portion is the *ileum.* These have no external mark to distinguish the one from the other. The jejunum is wider than the ileum, and its coats are thicker; the intestine tapers as it approaches the cœcum.

The whole intestinal tube is more or less completely covered by the serous membrane of the abdomen, *the peritoneum.* The duodenum above and the rectum below are least covered by it; the rest is almost entirely enveloped, a small portion being left uncovered where the blood-vessels enter the intestine, and where the peritoneum passes to the abdominal wall. Each portion of intestine is attached to the abdominal wall by a process of peritoneum, the duodenum and the rectum very closely, the rest more or less loosely. The process of peritoneum which connects

the small intestine to the spine is *the mesentery*, and each portion of the large intestine is connected to the corresponding region of the abdominal wall by a process of peritoneum, which is designated by prefixing the word *meso* (μεσος medius) to the name of the particular portion of intestine: thus *mesocœcum* is the process which connects the cœcum to the iliac fossa; *mesocolon*, right, transverse, left, is that which belongs respectively to the three portions of the colon; and the *mesorectum* connects the rectum to the concavity of the sacrum.

Attached to the colon are small processes of peritoneum, containing fat, and called *appendices epiploicæ*, from their resemblance to the *epiploon*, or great omentum, which descends from the great curvature of the stomach and from the transverse colon, like a curtain, in front of the small intestine.

The Intestinal Canal in Vertebrata.—The intestinal canal is disposed in the four vertebrate classes much on the same plan as in the human subject:—

In *Fishes* the intestinal canal exhibits for the most part a very simple conformation. In many fishes it passes quite straight or very nearly so, through the body: when it does exhibit convolutions they are few and short, and rarely to any great extent. A pyloric valve is generally present, separating the intestine from the stomach; immediately succeeding to this valve, the intestine generally experiences a dilatation, whence it gradually contracts to its terminal portion, which again becomes dilated. This portion corresponds to the large intestine, and commonly a valvular fold of the mucous membrane is present at its union with the preceding portion; it terminates in a cloaca common to it with the genital and urinary organs. In some fishes, however, no dilatation is found, nor any external distinction between the stomach and intestine, and the canal from the œsophagus to the anus is of uniform calibre. Immediately below the pylorus we very commonly find a series of tubular prolongations from the intestine, terminating in blind extremities. These constitute the *appendices pyloricæ* or pyloric follicles, which most comparative anatomists consider to supply the place of a parenchymatous pancreas. These appendices vary considerably in both number and size. In *pleuronectes flesus* there are only two very short ones, placed opposite each other at different sides of the intestine*; in *ammodytes tobianus* there is only one; in *Blennius* and *Gasterosteus* there are only two, so small that Wagner compares them to the follicles of the proventriculus of birds; there are from ten to thirty in many species of *Clupea* and *Salmo*, and in the genera *Gadus* and *Scomber* (the common mackerel, for example), there are as many as two hundred.† On the other hand, they are entirely absent in many fishes. Again in some they are simple, in others they become subdivided or branched at their blind extremities, and in others still these branches undergo subdivision, and the resemblance to the glandular formation is enhanced by the fact that these branchings are connected by means of cellular membrane and blood-vessels.

In *Reptiles*, the intestinal canal differs from that in fishes chiefly in having

* Figured in Carus's Anat. Comp. pl. ix. fig. 20.

† R. Wagner, Vergleichend. Anatom.

undergone a slight increase of developement. The division into large and small intestine is distinct throughout the class, and often an ileo-cœcal valve is present. In *Ophidia* the small intestine presents numerous short convolutions at acute angles; the large intestine ends in a cloaca. The intestinal canal is longest in the *Chelonia*, and next to them in the *Crocodiles*. In the *Chelonia* the line of distinction between the large and small intestine is not so distinct as in the rest, and the muscular coat is remarkable for its great thickness. The tortoises have a short, wide, and cylindrical cœcum, which is continuous without interruption with the large intestine: they have also a circular ileo-cœcal valve.* The great thickness of the muscular coat and the almost total obliteration of the canal during its contracted state constitute one of the most striking peculiarities of the intestine in Chelonian reptiles. In *Batrachia* the difference between large and small intestine is very distinct, being chiefly indicated by difference of calibre, and in frogs a circular ileo-cœcal valve; in the toad, however, there is a small cœcum, without ileo-cœcal valve. In most of the *Saurian* reptiles there is a cœcum according to Meckel, and generally an ileo-cœcal valve: in the Crocodile the valve is present but the cœcum absent.

In *Birds*, the intestinal canal, although longer than either in fishes or reptiles, yet retains considerable simplicity of form. It presents much variety in length and in the number of its convolutions, according to the food and habits of the bird. The duodenum, which immediately follows the gizzard, has always the form of a long fold, which contains the pancreas in it. The small intestine, more or less folded in different orders, terminates in a short and somewhat wide large intestine, at the commencement of which are two cœca, one on each side of the intestine. These cœca vary considerably in length from almost simple papillæform offsets, as in the Soland goose,† to processes three feet in length, as in the grouse. It sometimes occurs that there is only one cœcum. The large intestine is short and straight, and is continued from the termination of the small intestine, without fold, to the cloaca. There is connected with the small intestine an appendage, the remains of the duct of communication between the yolk-bag and intestine in the chick. In some birds this appendage, which is said to be devoid of a muscular tunic, is as large or larger than the cœca.

So much diversity exists in the form, length, and arrangement of the intestinal canal in the different orders of Mammalia, that it will be necessary briefly to state its peculiarities in each order.

In *Carnivora* we find examples in which the intestinal canal is remarkably short in relation to the length of the body. The small intestine has but few and simple convolutions; it opens into a short cœcum (convoluted, however, in the dogs) which scarcely differs in width from the rest of the large intestine. The proportion in the length of the intestinal canal to that of the body varies from, according to Meckel, five to one, as in the cats and dogs; to eight to one, and nine to one, as in the hyena and bear; or to fifteen to one as ascertained by Meckel in *Phoca vitalina.* The large intestine is shorter and wider than the small; it is cylindrical in form, not sacculated as in man and many others.

In *Insectivora* the intestinal canal is short, and without cœcum, the diameter being pretty uniform throughout. In *Sorex*, according to Meckel, its length is to

* Meckel. † Sir E. Home's Comp. Anat. pl. civ.

that of the body as three to one, in the hedgehog as six to one; in a mole examined by ourselves, which measured from snout to tail seven inches, the intestinal canal from pylorus to anus measured four feet three inches.

In the *Cheiroptera* a very marked distinction exists in the form of the intestinal canal between the frugivorous and insectivorous genera. In the former, as in *Pteropus*, it presents numerous coils, and is in length seven times that of the body —the cœcum is absent. In the latter the canal is extremely short, bearing to the length of the body the proportion of two or three to one as in *Vespertilio noctula*. Much variety exists as regards both the form and length of the intestinal canal in the *Edentata*. The distinction between large and small intestine is not evident in many of the genera. In the *Manis* and *Bradypus* there is no trace of a cœcum: on the other hand the two-toed ant-eater (*Myrmecophaga didactyla*) has, according to Daubenton and Meckel, two small and narrow cœcal appendages resembling those of birds, situated at the confines of the two portions of the intestine; the orifices of these cœca are so small that the fœcal matter cannot find its way into them. Mr. Owen has preserved in the Hunterian collection a specimen from the weazel-headed armadillo (*Dasypus mustelinus*), of two similar cœca between which the ileum terminates. The terminal aperture of this intestine is of a slit-like form, and from its position between the cœca it admits of being effectually closed by the lateral pressure of the contents of the cœca.*

Great length and wide calibre are the characteristics of the intestinal canal in *Ruminants*, *Solipeds*, and *Pachydermata*. In the sheep, which belongs to the ruminant order, the intestine is in length thirty times that of the body, and in the horse, according to a measurement made by us, the intestinal canal was eighty-seven and a half feet in length. There are numerous convolutions of the small intestines in each of these orders, and a large capacious cœcum, from which the wide and convoluted colon is continued. In *Ruminants* neither the cœcum nor the colon is sacculated by longitudinal bands, whilst both the *Solipeds* and *Pachydermata* exhibit the sacculated character in a very marked degree, and the bands of longitudinal muscular fibres are very highly developed, extending from the blind extremity of the cœcum to the rectum. There is no ilio-cœcal valve, properly so called, in these orders, but the passage from the ileum to the cœcum (a foot and a half long in the horse) is very much contracted, and its inner membrane thrown into six or eight thick longitudinal folds, which are closely applied to each other and keep the canal closed. The cœcum in each of the orders is very capacious; in the Ruminants, the capacity of this portion of intestine somewhat exceeds that of the fourth stomach according to Meckel. In the *Solipeds* the cœcum is still more capacious. Meckel asserts that it is capable of containing more than three times as much liquid as the stomach. In *Pachydermata* the cœcum is shorter and wider than in the other orders: it is, according to Meckel, less capacious than the stomach.†

The *Rodentia* have, in general, a very long and convoluted intestinal canal. The small intestine has a mesentery of considerable length; its calibre is small and pretty uniform throughout, being however largest superiorly. In most of the *Rodent* genera the cœcum is of very great size, and in some it occupies a large portion of the abdominal cavity; in the omnivorous rodents, however, as the rat,

* Catalogue of the Hunterian Museum, vol. i. p. 219, 729, A.

† See Sir E. Home's plates of the cœca of several mammiferous animals, plates cxiii. et seq. vol. ii.

the cœcum is of small dimensions. The whole large intestine is cellulated, the cells being formed by longitudinal fibres and circular constricting ones.

In the genus *Myoxus* (dormouse), the cœcum is entirely absent, the only exception, according to Meckel, to the presence of this cavity in the rodent order.

In the *Marsupiate* animals, the distinction between large and small intestine is clearly marked by the presence of a cœcum. The small intestine is long, and in some very wide; the cœcum is of moderate length and width, its capacity being much below that of the stomach.

The chief peculiarity of the intestinal canal in the *Monotremata* is to be found at its inferior extremity, where a cloaca exists common to the rectum with the urino-genital organs. A small cœcum separates the long and small intestine.

The *Cetaceous* mammalia have an intestinal canal of considerable length. The length of the canal in the zoophagous cetacea is to that of the body as eleven or twelve to one. (Meckel.) According to Cuvier, the proper whales have no division between large and small intestine, and consequently no cœcum. This is the case in the porpoise. In the *Balæna Rostrata*, however, according to Hunter, and in all the *Balænæ*, according to Cuvier, a small cœcum, not unlike that of carnivora, exists. In the herbivorous cetacea the intestinal canal is of proportionally greater length than in the zoophagous cetacea. In the *dugong*, according to Meckel, its length exceeds forty times, and in the *lamantin* of Kamschatka, twenty times that of the body.

The *Quadrumana.* The length of the intestinal canal in this large order of Mammifers presents very remarkable variety, which is the more curious as the nature of the food is, with few exceptions, similar in the various genera. The proportion of the length of the intestinal canal to that of the body is in some as eight to one, whilst in others it is only as three to one.* The division into two portions is effected in the same manner as in the human subject, and the general arrangement of both small and large intestine is very similar to those of man. A cœcum exists in all the genera, but presents considerable variety as to length; an increased length of this portion of intestine along with a larger developement of the splenic extremity of the stomach being employed in some cases to compensate for a deficiency in the length of the intestinal canal. The orangs and gibbons have the peculiarity, which they alone possess in common with man, of a process from the cœcum, some inches in length, denominated *the vermiform appendix.*

From the preceding brief review of the anatomical characters of the intestinal canal in the vertebrate classes, we gather, that this portion of the digestive tube diminishes in complexity as we descend from mammalia to fishes; that a short and simple intestinal canal is generally co-existent with a diet of animal food; and on the other hand, that a diet of vegetable food, or a conjoint animal and vegetable diet requires greater length and greater complexity in the form and structure of the intestines. In estimating the length of the intestinal canal we must not confine our examination to a mere external measurement, as we should thereby be led to a very erroneous conclusion. Deficiency in length, as measured on the exterior of the intestine, may be supplied by increased width—by a more highly-developed state of the villi of the mucous membrane—by numerous folds of that membrane, and the energy of the action of the mucous membrane on the contents of the intestine may be augmented by the greater number and size of the glands which pour

* Vide a table in Meckel's Anat. Comp. (French Ed.) tom. viii. p. 778.

out their secretions on its surface. It may further be observed, that as the several portions, whether of small or large intestine, have very definite characters as regards the mucous membrane, we can readily determine the relative length and developement of each portion, and thus deduce its proper degree of importance in intestinal digestion. But upon these points it is much to be regretted that we are greatly in want of precise information; we are persuaded that nothing would tend more to the correct determination of the office performed by each portion of the intestinal canal than a series of careful observations with special reference to anatomical characters on the intestines of a great number of animals.

Much importance is attached by Physiologists, and apparently with good reason, to the size and form of the cœcum. It is difficult, however, and in the present state of our knowledge impossible to determine the law which influences its developement. Nevertheless, it may be stated that there appears to be a direct relation between this developement of the intestine and the hardness of digestion of the food: in some instances we find that a large cœcum compensates for a less capacious stomach, as in the *Solipeds*, and in these cases there exists even a striking similarity in the forms of these two organs. A large cœcum, then, belongs to the herbivorous classes, as a large stomach does, and a small çœcum would, on the other hand, indicate a diet of animal food. Anatomy would seem to point to the conclusion that the function of the cœcum is not dissimilar to that of the stomach, and that in it substances hard of digestion are subjected a second time to a reducing action resembling that of the stomach. Perhaps the anomaly which we have noticed in the dormouse, in the absence of a cœcum, may be explained on the supposition that this accessory digestive cavity was rendered unnecessary in consequence of the existence of the glandular pouch at the cardiac orifice of the stomach in that animal.

The subdivision of the intestinal canal in man into the small and large intestine by the difference in calibre of those two portions of that tube as well as by the existence of an ileo-cœcal valve, has already been described. There are other characteristics, however, of anatomical constitution which likewise sufficiently distinguish them. The whole of the intestinal tube is composed of certain tunics which, enumerated from within outwards, are as follows:—1st, the mucous membrane: 2ndly, the submucous tissue; 3rdly, the muscular coat; 4thly, the serous coat, which is connected to the tunic last named by a thin layer of very delicate areolar tissue. Of these tunics the mucous membrane, the muscular coat and the serous coat, exhibit, on the whole, very distinctive characters in the two divisions of the intestine.

The mucous membrane continuous with that of the stomach exhibits very characteristic features in the different portions of the intestine. We shall reserve the description of it until we have spoken of the other tunics.

The submucous tunic is a layer of very fine areolar tissue, which connects the mucous to the muscular coat; it is entirely devoid of

fat, and presents the same characters throughout the whole intestinal canal. Placed immediately underneath the mucous membrane, it constitutes the medium, through which the various sanguiferous and other vessels and the nerves pass to that membrane.

The muscular coat of the small intestine consists of two layers or planes which differ from each other as regards the direction of their fibres. The external plane is composed of longitudinal fibres, continuous superiorly with the longitudinal fibres of the stomach; they form a continuous tunic surrounding the intestine, and extending from the pylorus to the cœcum. C. B. Albinus* states that they exist only as a band a finger-breadth broad, and corresponding to the concave border of the intestine along which the mesentery is attached, and to this he attributes the concavity which the inflated intestine presents towards the mesentery. We have no doubt, however, that the longitudinal fibres form a continuous tunic around the intestine, though they are strongest along the line of attachment of the mesentery, and are very apparent in that situation at times when they are indistinct elsewhere. The circular fibres are much more distinct than the longitudinal; the direction of which they cut at right angles. They surround the intestine in a circular manner, not spirally, as some anatomists have asserted.

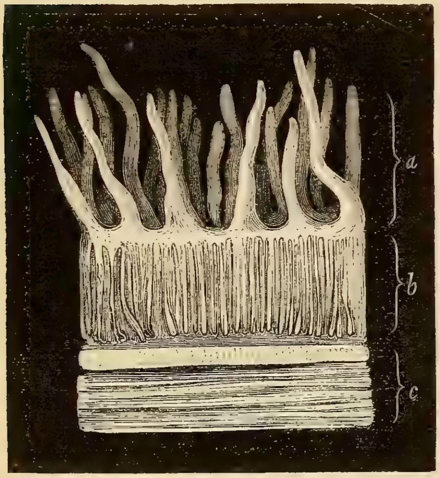
The muscular tunic of the large intestine is likewise disposed in two layers of fibres. The external, however, does not, as in the small intestine, form a uniform layer around the intestine, but is developed chiefly in three bands, about half an inch wide, with a few intervening longitudinal fibres. These bands commence at the root of the vermiform appendix of the cœcum, and extend in this form to the rectum where they become expanded and form a continuous tunic over the whole intestine. The longitudinal bands are shorter than the intestine; the effect of this is to produce a puckering of all its coats at certain intervals throughout the whole length of the colon. At these points the colon appears to be constricted, as by a shorter bundle of circular fibres, and its mucous membrane projects into the interior, forming large folds. These folds separate sacculated portions of the intestine, which are the *cells* of the colon, and the convex bulgings seen on the exterior of the inflated large intestine are the walls of these cells. The circular fibres are arranged in the same manner as in the small intestine, being spread uniformly over the surface of the intestine.

* Specimen Anatomicum exhibens novam tenuium Hominis Intestinorum Descriptionem. Lugd. Bat. 1724.

Of the Mucous Membrane of the Intestinal Canal.—The intestinal mucous membrane so far resembles that of the stomach, that it is of the *compound* variety (see *ante*, p. 162); and its thickness is caused by the involution of multitudes of tubes, which terminate in blind closed extremities, and rest vertically upon the submucous tissue. Most of the tubes remain undivided from their open to their closed extremities, some are bifurcated towards the blind extremity. Each tube has a separate orifice on the free surface of the mucous membrane, except in the upper part of the duodenum and in the cœcum, where they open by sets of three or more on the floors of shallow cells, as in the stomach. These tubes are commonly called Lieberkühn's *follicles;* but they were first described by Brunn, or Brunner, who has given a good delineation of them, and their real nature was not known to Lieberkühn, who regarded them as muscles.

In examining thin vertical sections of the mucous membrane from any part of the intestine, we see these tubes closely set parallel to each other; they are straight, and, excepting that here and there one is bifurcated, they exhibit no irregularity or bulging of their walls, and are pretty uniform in diameter throughout their length (fig. 157). All the elements of the mucous membrane contribute to their formation; the basement membrane, the epithelium, and the submucous tissue, which is sparingly interposed between them.

Fig. 157.



Section of the mucous membrane of the small intestine in the dog, showing Lieberkühn's follicles and villi.
a Villi. *b* Lieberkühn's follicles. *c* Other coats of the intestine.

The epithelium is columnar or subcolumnar; the cells are disposed in a single layer, with one end adherent to the basement membrane. The cast off particles often fill each tube as mucus, which escapes at the orifice on the free surface of the mucous membrane. These tubes are shorter in the large than in the small intestine; and as the thickness of the mucous membrane is dependent on their length, we find it less thick in the former

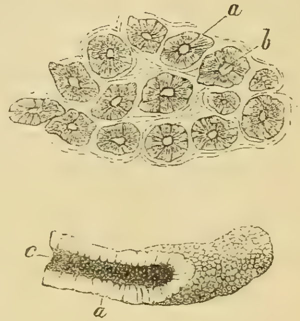
than in the latter intestine. The mucous membrane is thickest where the tubes are most developed, namely, in the jejunum.

Lieberkühn's follicles are doubtless secreting agents, resembling in that respect the tubes of the stomach. Probably their office, in reference to the intestinal contents, is the same throughout the whole intestinal tube, as they present everywhere so much uniformity of arrangement and structure, and as each portion of the intestine possesses other and peculiar glands. As yet, however, nothing is known respecting the nature of the mucus which is secreted by them.

Fig. 158.

A.

B.



A. Transverse section of Lieberkühn's tubes or follicles, showing the basement membrane and subcolumnar epithelium of their walls, with the areolar tissue which connects the tubes. *a*. Basement membrane and epithelium, constituting the wall of the tube. *b*. Cavity or lumen of the tube. Magnified 200 diameters.

B. A single Lieberkühn's tube, highly magnified. A happy accidental section in the oblique direction has served to display very distinctly the form and mode of packing of the epithelial particles, the cavity of the tube, and the mosaic pavement of its exterior. *a*. Basement membrane. *c*. Internal surface of the wall of the tube. Magnified 200 diameters.

By the infinite multitude of minute and microscopic involutions which form Lieberkühn's follicles, the extent of surface of the mucous membrane is enormously increased. It is still further enlarged by the existence of various folds and processes which project into the cavity of the intestine; these we shall now proceed to describe.

Of the Valvulæ Conniventes, Folds, and Villi.—The mucous membrane of the small intestine exhibits numerous folds, which, small, irregular, and resembling the rugæ of the stomach in the superior third of the duodenum, assume a much more definite form, and are much more highly developed in the remaining portions of the small intestine, but especially in the jejunum.

The irregular foldings of the upper portion of the duodenum very soon exhibit the tendency to assume a transverse direction with reference to the axis of the intestine. In the middle and inferior portions of the duodenum we find numerous transverse plaitings or folds from one-eighth to a quarter of an inch in depth. These are simple folds of the compound mucous membrane, including a process of the submucous areolar tissue—they are called *valvulæ conniventes*, from their valvular form, and from their movements under water resembling the flapping of valves, or the winking motion of the eyelids. Each fold passes round the intestine for

about three-fourths or five-sixths of its circumference, gradually diminishing in depth towards each extremity, but sometimes bifurcating and coalescing by one or both subdivisions with the fold above and below. In the lowest part of the duodenum, and in the jejunum, the *valvulæ conniventes* acquire their highest developement. Here they lie very close together, and many of them pass nearly round the intestine; they are deeper, also, here than elsewhere, being sometimes half or three-fourths of an inch in depth. In the ileum they gradually diminish in length and in depth, frequently not passing round more than one-half the circumference of the intestine, and measuring not more than one-fourth or one-eighth of an inch in depth; and in the lowest part of the ileum they almost entirely disappear.

It is remarkable that these folds are peculiar to the human subject. No other animal, so far as we know, exhibits any arrangement of transverse folds of the intestinal mucous membrane resembling them.

The folds of mucous membrane in the large intestine are the partitions between the cells of the colon; they exhibit much uniformity of shape although they vary very much in size; they are least developed in the sigmoid flexure.

At the junction of the ileum with the cœcum there are two folds which bound the slit-like aperture of communication between the small and the large intestine. These are the segments of the *ileo-cœcal valve.* The aperture is a simple slit which passes nearly horizontally from before backwards, and is bounded on all sides by mucous membrane. Its lower border is formed by the free edge of a deep semilunar fold of mucous membrane, enclosing submucous tissue, and a few circular muscular fibres; and another fold, of much less depth, but of similar shape and constitution, forms its upper lip. This latter fold has a more horizontal direction than the former, which is nearly vertical. The folds coalesce in front of and behind the aperture, and form small bands, called *fræna,* and which follow for a short distance the course and direction of the segments of the valve. The free margins of these two segments come in apposition in the distended state of the cœcum and close the aperture, or at least diminish and constrict it so much as, in general, to prevent the reflux of any but liquid or much-subdivided matters into the small intestine.

In the rectum there are folds of various sizes and directions, which are most numerous in the empty state of the gut, and are effaced by its distension. The late Mr. Houston, of Dublin, has

described certain permanent folds or valves, of semilunar shape, which he demonstrated by moderately distending the rectum with alcohol, which at the same time hardens its tunics, and thus displays their condition in the state of repletion. Three is the average number; but sometimes a fourth is found, and at other times only two are present. The largest and most constant valve is situated opposite the base of the bladder, about three inches from the anus. The fold next in frequency is placed at the upper end of the rectum; and the third occupies a position midway between these. When a fourth is present it is situated about one inch above the anus. In the empty state of the intestine these folds overlap each other, as Mr. Houston remarks, so effectually as to require considerable manœuvring to conduct a bougie or the finger along the cavity of the intestine. Their use seems to be "to support the weight of fæcal matter, and prevent its urging towards the anus, where its presence always excites a sensation demanding its discharge." *

Of the Villi.—Villi are minute processes of the mucous membrane of the small intestine, to which they are exclusively confined (fig. 157). They project from the free surface of the mucous membrane into the cavity of the intestines, and seem admirably adapted to become implanted, like so many little roots, in any semifluid or fluid material which may fill the bowel. Villi are first found in the duodenum, where they appear to develope themselves as elongations of the partitions between the cells into which Lieberkühn's tubes open. In the lower half of the duodenum, and the rest of the small intestines, they are very numerous, and give to the surface of the mucous membrane an appearance like that produced by the pile of velvet. They are continued down to the ileo-cœcal aperture, and cease abruptly at its margin, covering the surface of the valve-segments next the ileum, but being wanting on the cœcal surface.

A good view of the shape, arrangement, and number of the villi may be obtained by examining a piece of villous mucous membrane fixed under water. In man the villi are conical in shape, somewhat flattened, and measure in length from apex to base from the $\frac{1}{60}$th to the $\frac{1}{45}$th of an inch. They vary much in shape and size in the lower animals: in the dog, cat, and lion, they are long and almost filiform; in the sheep and rabbit they are small, flattened, and conical; in the turkey they are large and lamelliform. Most fishes and reptiles are devoid of villi.

In structure a villus resembles an everted Lieberkühn's follicle;

* Dub. Hosp. Rep. vol. v. p. 163.

the same elements exist in both, basement membrane, epithelium, sub-basement tissue, which occupies, along with vessels and perhaps nerves, the interior of the villus. The difference between the two structures is that the epithelium is in the interior of the follicle and on the exterior of the villus.

A single layer of the columnar epithelium covers each villus (fig. 159). The particles adhere by their sharp extremities to the basement membrane, and their bases, packed together, present on the surface an appearance of a pavement.

The basement membrane is readily seen when the epithelial layer falls off, which it is apt to do during the digestive process (fig. 160). It is a single layer of homogeneous membrane, beneath which, or in the cavity of the villus, are seen, in well-injected specimens, the blood-vessels of the villus.

Each villus is provided with a plexus of capillaries. A single artery enters its base, and, passing up its centre, forthwith breaks up into a capillary plexus, which is seen at all points of the surface of the villus, immediately beneath the

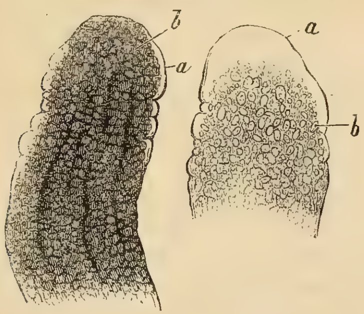
Fig. 159.

A. B.

A. Villi of duodenum of dog, two hours after death, showing the substance of the villus retracted from the epithelial investment, like a finger from a glove. The process of digestion was not going on at the time of the dog's death, as there was no food in the stomach nor chyle in the lacteals. Magnified 80 diameters.

B. From the same part, and same dog, showing the epithelium corrugated, being attached and free at intervals. Magnified 80 diameters.

Fig. 160.



A. B.

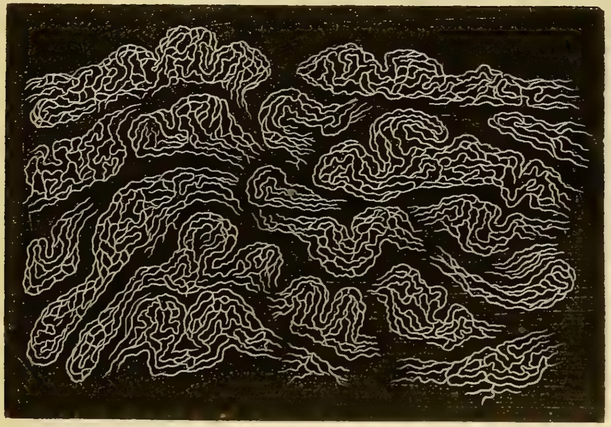
A. From the same part of another dog, fed $2\frac{1}{2}$ hours before death, showing the columnar epithelium stripped off, and the cellular substance of the villus covered merely by basement membrane. Magnified 200 diameters. *a.* Basement membrane, slightly raised. *b.* Cellular substance of the villus, disposed somewhat in columns.

B. From the same part and same dog, showing villus denuded of epithelium, and the basement membrane raised in a bulla by the endosmosis of water, in which it was immersed. Magnified 200 diameters. *a.* Basement membrane. *b.* Cellular substance of the villus.

basement membrane. From this arise at various points small veins, which pass out of the villus in one or more trunks (fig. 162).

The cavity of the villus also contains one or more small lacteals, in which originates the proper lacteal plexus of the intestine. The villi are seen white with chyle, during the absorption of that fluid, and the chyle may be fixed in them by coagulation, if the membrane is promptly immersed in alcohol. Respecting the manner in which these vessels are disposed in the villus, however, nothing certain is known. Some have described a net-work of these vessels extending to the extremity of the villus. The investigation is one of the most difficult in minute anatomy, and is highly important as bearing upon the mechanism of the absorption of chyle.

Fig. 161.

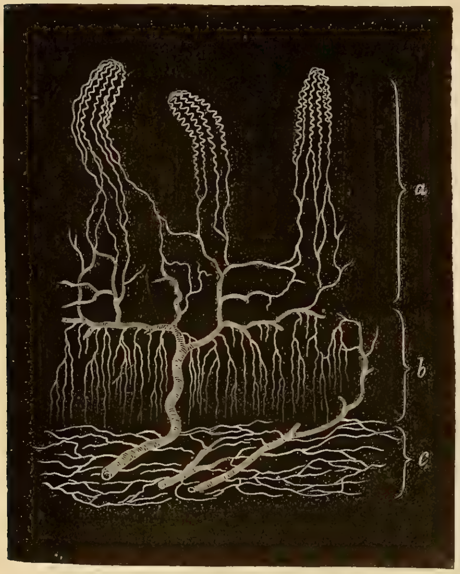


Capillary plexus of the villi of the human small intestine, as seen on the surface, after a successful injection, magnified 50 diam.

Nothing whatever is known of the relation of the nerves to the villi. The tissue which occupies the cavity of the villus, and which supports the capillary plexus, and whatever other vessels may exist in it, is a soft, imperfectly formed areolar tissue, containing nuclei and granules, and resembling somewhat the tissue contained in the gustatory papillæ of the tongue. That portion of it which corresponds to the free extremity of the villus differs from the rest; it exhibits a vesicular structure, and resembles very minute fat vesicles, filled by some transparent fluid. The tissue which occupies the remainder of the villus seems to consist chiefly of nuclei or granules, some of which present an indistinct arrangement in columns, which are parallel to the axis of the villus. During the process of chylification it appears to be the seat of some very remarkable changes connected with the absorption of chyle.

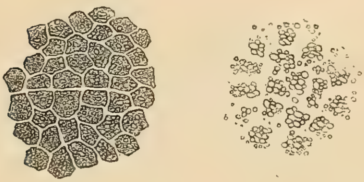
The function of the villi appears evidently to be connected with absorption, and specially with the absorption of chyle. This view rests upon the following grounds:—First, that the villi exist only in the small intestine, where the most active absorption of digested matters evidently goes on; and that they are most highly developed and most numerous in that part of the small intestine where chyle is first formed. Secondly, that during the process of chylification the villi are turgid with blood, and obviously present all the appearance of being the seat of some active vital process; they are enlarged and opaque, apparently from a change in the intravillous tissue, and probably also from the introduction of some new matter into them. In animals that have been kept fasting for some time prior to death the villi look small, and as if shrunken within their epithelial sheaths, which, in some instances, adapt themselves to the diminished size of the enclosed villi, by becoming thrown into folds. (Fig. 159.) But during the digestive process the villi are large and full; the nuclei of their proper tissue are very distinct; the basement membrane is here and there bulged by them on the surface, especially towards the

Fig. 162.



Vertical section of the coats of the small intestine of a dog, showing only the commencing portions of the portal vein and the capillaries. The injection has been thrown into the portal vein, but has not penetrated to the arteries. *a.* Vessels of the villi. *b.* Those of Lieberkühn's tubes. *c.* Those of the muscular coat.

Fig. 163.



A. B.

A. Epithelium detached, and free in the cavity of the duodenum taken, immediately after death, from a dog fed $2\frac{1}{4}$ hours before. Each cell is filled with apparently fatty matter, partly granular and partly in globules. Magnified 600 diameters.
B. The same, suffered to stay an hour or two under the microscope, showing the fatty material aggregated into larger globules, the rest of the cell-structure having become indistinct.

free extremities, and the peculiar vesicular structure at the apices of the villi is compressed, or otherwise concealed from view or altered in character. (Fig. 160.) Lastly the epithelium seems to adhere much less closely to the villi during chylification than during fasting; and the epithelial particles themselves appear to undergo some change during this process. This latter change is represented in the annexed cut (fig. 163); the epithelial particles appear larger, their contents more distinct, and consisting of minute fatty grains as well as of some small globules.

Of the Glands of the Intestine.—These are, in addition to the Lieberkühn's tubes or follicles already described, and which are themselves secreting organs: 1. Brunner's or the duodenal glands; 2. the solitary glands; 3. Peyer's glands, or *glandulæ aggregatæ.*

Brunner's glands belong properly to the duodenum. They were discovered and described by J. C. Brunn in 1686. We find them in the submucous areolar tissue, disposed as a more or less thick layer of whitish grains, immediately beneath the mucous membrane. They may be compared to the elementary grains of a salivary gland spread out on an expanded surface, instead of being collected into a mass. Near the pylorus they are most numerous, and most closely set and largest; towards the termination of the duodenum they become much fewer, smaller, and scattered; and nothing resembling them is found in any other portion of the intestine. They are much more developed in the Herbivora than the Carnivora; in man they are large and numerous, generally speaking, but exhibit a good deal of variety in different subjects, and in the very old they appear to have wasted and shrunk.

Fig. 164.

Vertical section of the mucous membrane of the duodenum in the horse, slightly magnified, showing, *v*, villi, *b*, *c*, mucous membrane and submucous tissue. *g*. Brunner's glands cut vertically, and a little spread out, showing their lobulated structure.

In point of structure Brunner's glands resemble precisely the pancreas. Their ultimate elements are bunches of vesicles which contain globular epithelium, and from which ducts arise which coalesce and form larger ducts, through which the secretion is poured into the duodenum. The exact relation of these ducts to the tubes of Lieberkühn is not known.

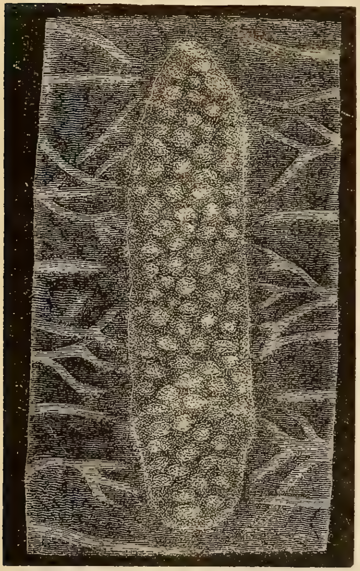
Brunner's glands, no doubt, secrete a fluid similar, perhaps, in

nature to the pancreatic fluid, which exercises an influence on that portion of the digestive process which takes place in the duodenum. Their restriction to the upper portion of the intestine, and their mode of arrangement in an expanded form beneath the mucous membrane, establish for them an analogy with the buccal glands, which are similarly disposed beneath the mucous membrane of the mouth, and which bear to the salivary glands the same relation as the duodenal glands do to the pancreas.

Fig. 165.

A solitary gland from the small intestine of the human subject magnified. After Boehm.

Fig. 166.



A patch of Peyer's glands of the adult human subject, from the lowest part of the ileum. After Boehm.

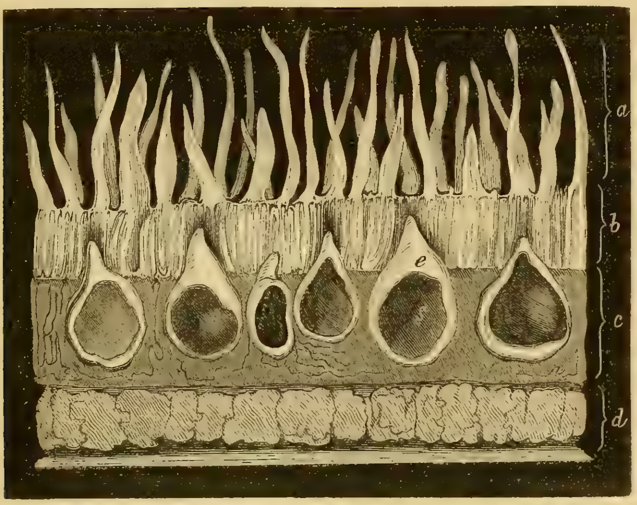
These glands, restricted as they are to the upper portion of the intestine, give a character to it of a physiological kind, and therefore more definite than any external boundary. Accordingly, while the duodenum may properly give its name to these glands, so the presence and extent of them should denote that portion of intestine which may be called duodenum, and define its limits.

The *solitary glands* are found in all parts of the intestine, but are most numerous in the jejunum, in the cœcum, in the vermiform appendix, and in the rest of the large intestine. When filled with their secretion they are like small grains, about as large as those of mustard-seed, placed beneath the mucous membrane in the submucous tissue, which cannot in those situations be inflated; they may be readily seen by holding up the intestine against the light. When empty and collapsed they are not easily discovered, and therefore are frequently overlooked.

One of these glands is a simple vesicle, or sacculus, of membrane, shaped like an India-rubber bottle, with a narrow extremity corresponding to the surface of the mucous membrane,

and a rounded, obtuse base imbedded in the submucous tissue. Its precise relation to the elements of the mucous membrane cannot be exactly determined; its wall seems to be formed of a structure distinct from the basement layer of that membrane. It projects among Lieberkühn's tubes, and, in the small intestine, is concealed and covered by the villi of the mucous membrane. Within it is contained a variable quantity of nuclei and granular particles, which, in the present state of our knowledge, must be viewed as a secretion. How this secretion is discharged is a matter of uncertainty, as no orifice has as yet been clearly demonstrated, hence some anatomists regard these glands as closed vesicles, which burst when distended to a certain point.

Fig. 167.



Vertical section through a patch of Peyer's glands in the dog.—*a* villi. *b* tubes of Lieberkühn, with the apices of Peyer's glands. *c*. Submucous tissue with the glands of Peyer imbedded in it. *d*. Muscular and peritoneal coats. *e*. Apex of one of Peyer's glands projecting among the tubes of Lieberkühn. The glands are seen laid open by the section. Magnified about 20 diameters.

*Peyer's glands.** — These may be regarded as aggregations of solitary glands, forming circular or oval patches situated on the free border of the intestine (fig. 166). They belong particularly

* The glands, so long known by this title, may be called "Grew's glands" with as much justice. They were discovered in several animals by our countryman, Dr. Nehemiah Grew, who also delineated them with great accuracy, and described them in his lectures to the Royal Society, in the year 1676, before Peyer's book was published (1677). Dr. Grew's descriptions and delineations may be found in an essay appended to his catalogue of the museum of the Royal Society, of which he was Curator, entitled "The Comparative Anatomy of the Stomach and Guts begun." See the advertisement prefixed to this work.

to the ileum, and ought to be regarded as forming a special anatomico-physiological feature of that portion of the intestine, and as indicative of its proper limits. We find in man as many as from seventeen to twenty-two patches, but with great variety both as to number and size. The patches are smallest towards the jejunum, and increase considerably in size towards the cœcum, so that some quite near the latter intestine measure from two to four inches in their long diameter.

Each of the small glands, the aggregate of which constitutes the patch of Peyer, is placed in a depression and surrounded by a groove resembling that which surrounds the papillæ vallatæ of the tongue; some being enclosed by a circle of the orifices of large tubes of Lieberkühn. It seems to be in every respect similar, as regards its intimate structure, to the solitary glands, and probably discharges its secretion by a similar mechanism. The arrangement and structure of these glands are well seen in a vertical section, as represented by fig. 167.

Peyer's glands are well developed in the Carnivora, more so than in Herbivora, and they commence very high up in the intestine, whence it would appear that the shortness of the small intestine which distinguishes the former animals is due to the imperfect developement of the duodenum and of the jejunum.

The office of these glands is involved in great obscurity; most probably it is connected with the further reduction of the alimentary matters as they pass through the intestine. But we are unable to form any conjecture as to the causes which determine the peculiar shape or position of the glands, or as to the nature of their secretion. They are larger and more developed during the digestive process than during fasting, a fact which denotes that the former is the period of their greatest activity of function. It is not impossible that the peculiar odour of the fæces, which is in a great measure characteristic in particular classes of animals, may be due to a secretion by these glands.

In typhus or typhoid fever these and the solitary glands are prone to become inflamed and to ulcerate. The poisonous matter which generates the fever is apt to fix on these glands; or they may be the special channel for its elimination, and in the process they suffer irritation. In phthisis these same glands are very liable to become the seat of the tubercular deposit, and also of an ulcerative process, whence results the diarrhœa, which proves so troublesome an accompaniment of that disease.*

* Some excellent remarks on the structure of the solitary and Peyer's glands

In Asiatic cholera all these glands become greatly enlarged from the accumulation of a large quantity of granular matter in the vesicles.

Brunner's glands exhibit a remarkable immunity from disease, and in this, as in other respects, they resemble the pancreas.

In concluding the account of the anatomy of the intestinal tube, the following summary of the special characters of each portion of it will serve to indicate more clearly what we have alluded to above,—that the physiological anatomy of the mucous membrane affords the best basis for its subdivision into portions, each of which, no doubt, exercises its special function in the digestive process:—

In the *duodenum* the mucous membrane exhibits, 1. cells and tubes like pyloric cells, gradually passing into straight Lieberkühn's tubes, which exist throughout the rest of the gut; 2. villi commencing in the upper part by the elongation of the septa between the cells, the villi becoming extremely numerous and crowded together in the inferior two-thirds; 3. in the lowest third a few solitary glands; 4. Brunner's glands very numerous in the upper part, gradually diminishing in size and number below; 5. valvulæ conniventes well developed in the inferior half.

The orifice by which the biliary and pancreatic ducts open into the intestine, is placed where Brunner's glands have either become very few or have ceased. In most of the Carnivora which we have examined these ducts open below the region of Brunner's glands; the point at which they pour their contents into the bowels has therefore no constant relation to the duodenum, if, as it is convenient to do, we may make the presence of these glands the characteristic mark of that portion of the intestine.

In the *jejunum* the mucous membrane is characterized by, 1. Lieberkühn's follicles and villi well developed; 2. valvulæ conniventes larger and more complete than elsewhere; 3. solitary glands.

The *ileum* exhibits, 1. Lieberkühn's follicles and villi well-developed down to the ilio-cœcal valve; 2. valvulæ conniventes, which gradually diminish towards the termination of the ileum and disappear; 3. solitary glands; 4. aggregate glands, or Peyer's patches, which are small at the upper part of the ileum, but greatly increase in size at its lowest portion.

may be found in a paper by Dr. Handfield Jones, "On the Intestinal Mucous Membrane."—Lond. Med. Gazette, 1848.

The mucous membrane of the *cœcum* and of the *whole large intestine* is distinguished by the complete absence of villi; by the presence of Lieberkühn's follicles and of solitary glands of large size, which are numerous in the vermiform appendix, as well as in the cœcum itself; and by the folds which form the partitions between the cells of the colon, as well as by the valvular folds of the rectum.

Movements of the Intestines.—The substances which enter the intestinal canal from the stomach are moved onwards by means of what is called the peristaltic, or the vermicular action of its muscular coat.

This action of the intestines is very conspicuous in animals opened immediately after death; under these circumstances it is probably in an exaggerated state owing to the stimulus created by the entrance of cold air into the abdomen. It may be displayed in a highly active state by subjecting the intestinal canal of an animal just dead to the influence of the magneto-electric machine, by the successive shocks of which this action becomes greatly increased in intensity and rapidity, though not altered in character.

In dogs and cats, in which we have most frequently observed the peristaltic action, it seems to commence at the pyloric third of the stomach, whence successive waves of contraction and relaxation (the former being instantly succeeded by the latter) are propagated throughout the entire length of the small and large intestines. The advance of the waves is always downwards. In examining a portion of intestine at the moment of its contraction, we perceive a dilatation above it as well as below it; the latter being produced by the protrusion into it of the contents of the now contracted portion of intestine; the former by the relaxation of a previously contracted portion. The rapid succession of these contractions and relaxations gives to the movements of the intestines the appearance of the writhings of a worm, whence they are distinguished by the appellation *vermicular.* Sometimes we have opportunities of observing these movements during life in man, in cases of extreme attenuation of the abdominal parietes; or in cases where, from some great obstruction in the course of the alimentary canal, the peristaltic action is very much increased in intensity above the seat of the obstruction; or in wounds of the abdomen; or during surgical operations.

There are certain facts which justify the supposition that this vermicular action has a proper rate of speed in each individual, and

that substances introduced into the highest part of the intestinal canal take a certain time, varying in each particular case, to traverse it. For example, the act of defæcation will, if allowed or encouraged, take place with the utmost regularity every twelve or twenty-four hours, and the quantity discharged will exhibit but little variation, the quantity and quality of the food remaining the same; and indigestible substances taken with the food, seeds, husks, skins, &c., will at certain intervals appear in the fæces, having traversed the whole canal. There is no act of the animal economy more strikingly under the influence of habit, *i. e.*, under the control of physical causes, without mental interference, than this of defæcation; nor, on the other hand, is there any act which may be more completely deranged by its being *baulked*, through the resistance which the will can oppose to it. The intestinal movements are partly due to the influence of the stimulus of distension upon the muscular tunic, and partly to the reflex action of the ganglia of the intestinal portion of the sympathetic, stimulated by the contact of the intestinal contents with the mucous membrane. Direct irritation of the solar plexus, or of the semilunar ganglia produces a marked increase in the movements of the intestines. (*Vide* p. 145, vol. ii.)

When obstruction exists at a certain point of the bowels, they become dilated above that point, and when the dilatation has attained a certain amount, their contents are found to flow back into the stomach, and are ejected by vomiting. This is commonly supposed to be due to an inverted direction of the action of the muscular tunic of the intestines (antiperistaltic action). But Dr. Brinton has very ably shown that there is no antiperistalsis of the bowels under these circumstances, any more than of the stomach in vomiting, and that the altered course of the fluids is due simply to their reflux along the axis of the intestine from the seat of obstruction. The muscular coat of the bowels acting in the downward direction, and with force proportionate to the obstacle, propels the fluids to a point where they encounter insuperable resistance, and whence they must take the course which affords least or no obstacle. Thus a backward current is established in that part of the fluid least influenced by the walls of the intestine, that, namely, which occupies its axis, or in Dr. Brinton's words, "*an axial reversed current* is developed, which returns matters from the neighbourhood of the strangulation to some higher point in the canal." When fluid returns along the sides of a syringe with a piston not water-tight, we have a somewhat analogous phenomenon, and we may imitate the reversed movement of the intestinal fluids by trying to

push water through an obstructed syringe, the piston of which is perforated in the centre, as illustrated by the annexed woodcut (fig. 168).*

Fig. 168.

Diagram to illustrate the formation of a backward axial current, in pushing water through an obstructed syringe with a piston perforated in the centre.

The contents of the intestine are moved on, portion by portion, much as in œsophageal deglutition. And, in their progress, they are mingled with fluids poured out from the intestinal mucous membrane.

Changes in the Mucous Membrane during intestinal digestion.—During intestinal digestion the mucous membrane exhibits an increased nutrient activity, as evinced by a greater afflux of blood, and by free secretion, as well as absorption; in connexion with which last function it exhibits peculiar changes, which must be specially noticed. It is red, moist, and covered with a more or less abundant mucus, &c.

The most remarkable change which takes place in the mucous membrane of the intestinal canal is observed in that portion of it which is covered by villi; that is, throughout the small intestine, especially below the point of entrance of the hepatic and pancreatic ducts. The villi are the agents of a peculiar process of absorption; and the changes which take place in them at this period appear to have immediate reference to the part which they perform in this function. They become enlarged and turgid, partly owing to an increased afflux of blood to them, and partly in consequence of a change which takes place in the intra-villous tissue, whereby the component nuclei and granules acquire an increase of size, and some of them arrange themselves in lines passing from the free extremity to the base of each villus (fig. 160, A). These lines appear to proceed from an accumulation of small cells formed at the free extremity of the villus within its cavity (fig. 160, B *b*): they are quite opaque, and their structure is, therefore, impenetrable to high powers in the microscope: they coalesce at the base of each villus, beyond which we have not succeeded in tracing them.†

* Contributions to the Physiology of the Intestinal Canal, *loc. cit.*, a highly ingenious and interesting paper.

† The phenomena here described were observed in dogs and cats fed in the ordinary way upon meat, milk, &c.

At this period an abundant quantity of loose epithelium is in contact with the mucous membrane, and surrounds the villi; and the sheaths of the latter seem to adhere very loosely to them, and may be much more readily detached than when the digestive process is not going on.

Mingled with the abundant mucus of the intestine, we find at this period very numerous white flocculi of a soft, loose, curdy material, the whiteness of which is conspicuous in the midst of other matters, which are more or less coloured from intermixture with bile. And, at the same time, the plexus of lacteal vessels, which is formed beneath the mucous membrane, and from which the larger lacteal vessels proceed through the mesentery to the mesenteric glands, is filled with a white fluid of the exact colour and appearance of milk, commonly called *the chyle.*

The display of the lacteal vessels filled with white chyle, at this period, is one of the most interesting sights among the many wonderful objects which engage the observation and the attention of the anatomist.

The white flocculent matter is most abundant in the duodenum and jejunum, and there the villi are most numerous; thence, likewise, proceed the greatest number of lacteal vessels. Lower down in the small intestine the flocculi gradually become less and less numerous, and ultimately disappear, the contents of the intestine consisting of a more or less fluid mass, apparently homogeneous, and coloured by bile. At the same time the villi become fewer and smaller, the number of lacteal vessels diminishes, and the glandular apparatus of the intestinal mucous membrane is more developed and distinct.

The occurrence of the flocculent matter, in that part of the intestine where the absorbing organs and the chyliferous vessels are most numerous, denotes that it must be regarded as constituting the nascent condition of that fluid which at this period fills the lacteal vessels and gives them their white colour—the chyle. It appears like a precipitate from the general mass of the intestinal contents, and many distinguished physiologists have regarded it in that light, and have attributed its precipitation to the addition of the biliary and pancreatic fluids to the chymous mass which has been pushed on from the stomach into the intestines.

This flocculent matter consists of a multitude of minute molecules apparently of a fatty nature (as they disappear under the action of ether), mingled with larger oil-globules, and also of numbers of particles of columnar epithelium, containing within them

several fatty molecules of large size, readily distinguished by their highly refractive power. The contrast between the epithelial particles obtained from this flocculent matter, and those of the intestine of an animal that had fasted for some time before death, is very striking, and indicates that they undergo a change during chylification, either connected with the absorbing process or with the transformation of the alimentary substances. (Fig. 163.)

Of the peculiar mechanism by which this nascent chyle is introduced into the lacteal vessels, and of the nature of the changes which it undergoes in them to form perfect chyle, we can form no adequate idea in the present state of our knowledge. We do know, however, that the material before its entrance into the vessels is very different from what it becomes after its introduction; and that in its advance towards the centre of the absorbent system it undergoes further changes, all of which tend to assimilate it more nearly to the blood itself.

Of the Chyle.—If, as seems most correct, we apply the term chyle to the fluid contained in the lacteal vessels during and shortly after digestion, we must make the distinction between *white* chyle and *transparent* chyle. The white chyle is a milk-like fluid, homogeneous in appearance, which, on being withdrawn from the lacteals and allowed to stand, separates, as blood would do, into serum and a clot. This clot consists of fibrine, which entangles, by its coagulation, certain particles proper to the chyle. These are chyle-corpuscles or globules, in every respect similar to lymph-corpuscles, and an infinite multitude of particles of extreme minuteness, to which Mr. Gulliver has given the name of *molecular base* of the chyle. These particles consist of fatty matter in a state of extreme subdivision.

During fasting, and also during the digestion of food wholly devoid of fat, the fluid contained in the lacteals is perfectly transparent and colourless, and not to be distinguished from the lymph of the lymphatics. In this fluid there is no molecular base, while all the other elements of the chyle are present. Hence there can be no doubt that the white colour of the chyle is due to the presence of the molecular base.

The chyle may exhibit various degrees of milkiness, according to the quantity of the molecular base. The white chyle, therefore, is chyle with molecular base in greater or less quantity; the transparent chyle is devoid of molecular base. Both kinds of chyle consist of a *liquor chyli*, essentially the same as the *liquor sanguinis* holding suspended in it chyle globules in the transparent-chyle,

and in the white-chyle, chyle globules, fat globules and molecular base.*

It would seem to follow, from observing the changes which the food undergoes in the small intestine, that the immediate office of that portion of the intestinal canal is to form this chyle; and it appears probable that the secretions poured into the small intestine from the glands, especially the liver, pancreas, and the glands of Brunner, which communicate with it, exercise a chemical influence upon the alimentary matters whereby this material is formed. We shall see further on that this view, receives strong support from the results of experiments and observations respecting the functions of the pancreas and liver.

Changes of the food in the small Intestine.—It remains now to inquire whether all the digestible food which passes from the stomach undergoes the change into chyle, or whether certain parts of it only are simply dissolved and pass by absorption directly into the portal blood, as in the stomach, whilst other parts are converted into chyle, and enter a different part of the circulation through the lacteal vessels. In other words, is it necessary that all food, prior to its appropriation by the blood as nutriment, should pass through the condition of chyle?

As it has been shown that the stomach can absorb certain fluids and dissolved solids, through the absorbing power of its blood-vessels, there can be no good reason for denying the same power to the intestines, which have a vascular system precisely of the same kind as that of the stomach. Now the substances which the stomach completely dissolves and absorbs, are the azotized aliments: it seems not unreasonable to conclude that such portions of these aliments as have escaped absorption by the stomach, may undergo a similar solution in the intestines, and be absorbed by their blood-vessels without passing through the state of chyle.

But to answer this question accurately we must determine precisely the changes which each kind of food undergoes in the intestine.

Bouchardat and Sandras have obtained from their experiments results which indicate that fibrine does not undergo the change into white chyle. They fed animals with fibrine, coloured with saffron or cochineal, and were unable to detect any trace of the colouring matter in the chyle. They found, likewise, that the contents of the lacteal vessels of animals kept fasting differed in no respect from that of animals fed on fibrine. These experiments, therefore, render it highly improbable that fibrine contributes to the

* See the Chapter on ABSORPTION.

formation of white chyle, and Tiedemann and Gmelin had long since found, that the quantity of fibrine contained in the lymph and chyle, after a long fast, is not less than that which is found there after digestion. Bouchardat and Sandras obtained the same results in their experiments on animals fed on albumen, casein, or gluten, as on animals fed with fibrine; these substances, therefore, must likewise be excluded from the list of those which are capable of forming chyle. Hence the whole class of neutral azotised substances, admitting of solution by pepsin, may be absorbed without passing into the state of chyle.

Neither does it appear to be necessary for the appropriation of amylaceous aliments that they should pass into the condition of chyle. These substances are but little digested in the stomach, and undergo their principal changes in the small intestines. Here the pancreatic fluid exercises a similar influence upon them to that which the neutral azotised matters experience from the gastric juice. Bouchardat and Sandras found that a few drops of pancreatic fluid, added to some boiled starch, and kept at the temperature of from 95° to 104°, dissolved it in a short time, the liquid became transparent, and all trace of starch disappeared. The same effect is produced if a piece of the pancreas be used instead of the pancreatic fluid.*

The starch in these experiments is converted into dextrine, or into sugar, in which state it is soluble, and thus admits of direct absorption into the blood-vessels, or the sugar undergoes a further change into lactic acid, and in this condition passes into the circulation. It appears that the presence of a free alkali is as necessary for these changes, as that of acid is needed for the solution of the neutral azotised substances. If the pancreatic fluid be acidulated, it ceases to act on starch, but, according to Bernard and Barreswil, acquires the power of dissolving albumen, fibrine, &c. We do not, however, find that alkalized pepsine is capable of dissolving amylaceous matters.

Bouchardat and Sandras have examined the changes which

* Dextrine is a substance having some of the properties of gum, and obtained from starch by the action of heat, diastase, or dilute acids. It is soluble in water, and exists in almost every part of plants. When starch is boiled in water for some time an abundance of dextrine is produced. If the action of diastase or of the acids be continued too long, or if the quantity of either be too large, grape-sugar is produced. Hence dextrine may be regarded as the first stage in the transformation of starch into sugar. The formula for dextrine is C^{12}, H^{10}, O^{10}. See Mulder's Chemistry of Animal and Vegetable Physiology, by Johnston, p. 224.

starchy substances undergo in the stomach and intestines in dogs. Man and carnivora are unable to digest raw starch in the stomach or intestines. Raw potato-starch introduced in a muslin bag into the stomach through a fistulous opening in the walls of the stomach, and withdrawn after a sojourn of twenty-four hours in that viscus, showed no sign of any change, nor did the gastric juice out of the body, the mixture having been kept at a high temperature for the same time, exert any influence upon the starch grains. When dogs were made to swallow raw starch, the grains were afterwards found intact in every part of the intestinal canal. Rabbits and granivorous birds, however, were found to possess the power of digesting raw starch, although more slowly than that which had been cooked. But this power was found to reside mainly in the upper part of the small intestine, and as the grains of starch became gradually fewer as the food descended in the intestinal canal, it seems reasonable to believe that each succeeding portion exercises a certain digestive power over them. In birds the digestive power of the small intestine was greater than in rabbits, the lower part of the intestine in the former exhibiting no traces of the starch grains. In the upper part of the small intestine, sugar and dextrine were found, and the lower the contents had passed down, the more did all traces of starch disappear.

Boiled starch is more readily digested by all animals than raw; to the carnivora and to man, cooking is essential to its perfect digestion. The same changes take place in it as in the raw starch, *i. e.*, it seems to undergo conversion into sugar, dextrine, and lactic acid. This change, however, is very slow and gradual, and although it occurs chiefly in the upper portion of the intestine, it is found taking place throughout the whole canal. The rapid formation of sugar in the intestinal canal leads to a proportionally rapid absorption of it, and to the elimination of it by the kidneys. It is apparently to guard against this, to protect the kidneys against the irritating influence of this substance, that the change of the starch into sugar and dextrine goes on with great slowness throughout the whole intestinal canal.

Our own experiments have yielded results similar to those of Bouchardat and Sandras, and confirm their conclusion, that neither azotised matters nor amylaceous substances contribute to form the true white chyle. At least it may be affirmed, that when animals are fed on such food, carefully freed from all oily or fatty matters, the fluid which is found in the lacteal vessels is perfectly transparent, and in all respects identical with that which is found in

them after a long fast. We select the following experiments in illustration of this statement:—

Exp. 1.—A cat was fed on horse-flesh, carefully freed from fat, on the 7th of July, 1848. On the two subsequent days it was fed on the whites of eggs, freed from yolk; and on the 10th, it was fed on the whites of five eggs, at nine o'clock A.M. At half-past one P.M., on the same day, it was killed. The thoracic duct was filled by a perfectly limpid chyle, which exhibited no molecular base, a few chyle-corpuscles, and a few blood-corpuscles. The lacteals were with difficulty visible in consequence of the transparency of the fluid by which they were filled. The stomach and duodenum contained pieces of softened albumen, as well as a considerable quantity of a soft homogeneous jelly-like mass. In the latter intestine the villi were covered with epithelium, and did not exhibit any appearance to indicate that they were the seat of an active process of absorption.

Exp. 2.—A small healthy terrier was fed at nine A.M. with half a pound of wheaten bread, having previously fasted twenty-four hours; it was killed at one o'clock on the same day. The thoracic duct was filled with a clear fluid, which, when collected on a slip of glass, exhibited a faintly reddish hue. Under the microscope it was found to exhibit numerous red blood corpuscles, with a much smaller number of white corpuscles, but more than the usual proportion for blood. No *molecules* were perceptible. The fluid, when collected in a watch-glass, coagulated in two minutes into a firm clot. A small quantity of softened bread was found in the stomach, and a still smaller quantity of the same bread very much softened, liquid, diffused, and coloured by bile, was found in the duodenum. In both the contents were acid. The villi were covered with epithelium, which adhered firmly to them, without any great opacity of their interior, or other indication of activity of function. On chemical examination by our friend, Mr. Lionel Beale, junior, a highly competent analyst, the contents of the stomach were found to consist of a small quantity of sugar, with a good deal of starch, while in the duodenum sugar existed in great abundance, and the starch only in very minute quantity.

Exp. 3.—A similar dog to the preceding was fed at the same time with two ounces and a half of horse-flesh, and the same quantity of beef suet; it was killed four hours and a half after having been fed. The whole lacteal system was distended with a white milky chyle, which, under the microscope, showed a large quantity

of *molecular* matter, as well as red and white blood corpuscles. The contents of the intestine were more or less acid throughout, and abundantly coloured by bile. There were very numerous white flocculi, most conspicuous in the duodenum, and becoming gradually less numerous to within an inch or two of the cœcum, where they ceased. These flocculi consisted of an abundance of granular matter, with columnar epithelium, having the free ends of the particles filled with minute oil-globules, while the neighbouring epithelium contained no oily matter. The villi were mostly stripped of their epithelial sheaths, or held them very loosely; the intra-villous structure was opaque, and the vesicular structure beneath the basement membrane at their free extremities was very distinct.

It was evident in these experiments that the marked contrast between the state of the contents of the lacteals, and the condition of the villi, was connected with the presence or absence of fat in the food, and that so long as the food was purely albuminous or fibrinous, or mainly amylaceous, the chyle was transparent, and the villi apparently inactive; but that the addition of fat to the food called the villi into activity, and filled the lacteals with an abundant milky chyle.

Are we to infer then that the lacteals absorb fatty matters only, and that the villi are altogether inactive, save when fatty or oily substances are to be absorbed? We apprehend that such an inference is not justifiable; it may, however, be concluded that the villi and the lacteals are capable of absorbing all substances which the blood-vessels absorb, and by a simple process; but that the absorption of fatty matters devolves upon them only, and is a more complex process, involving considerable changes in their tissue.

And upon similar grounds we may conclude that while albuminous and fibrinous aliments contribute to the formation of chyle, they do not necessarily undergo the change into chyle in order to be absorbed. But fatty matters appear to admit of absorption in no other way, except by a reduction to the state of molecular base of the white chyle.

These observations and experiments denote sufficiently clearly that two channels exist for the transmission of the nutritious matters from the intestines to the blood; one through the lacteals by the villi; the other directly through the walls of the blood-vessels themselves. Matters taking the latter route must pass through the liver and would be subjected to the influence of that gland before they reach the *inferior* vena cava and the right auricle, while those

passing through the former channel must permeate a totally distinct system of vessels, namely, the lacteal system, to be conveyed to the *superior* vena cava and to the right auricle, where, having mingled with the blood coming from the liver, both are transmitted by the right ventricle to the lungs.

And it would seem that the object of the two modes of absorption at the intestine, and of the two paths of transmission from the intestine to the centre of the circulation, is to keep separate, up to a certain point, two kinds of material resulting from the digestion of the food. And probably the reason why one kind of product is reserved to pass through the intricate capillary plexuses of the vascular system of the liver, to the exclusion of the other, is because it contains material out of which the liver may elaborate bile; whilst the other material is transmitted through a less complicated series of channels more directly to the lungs.

Of the offices of the Pancreas and Liver in Digestion.—The presence of two such great glands as the pancreas and the liver existing in a large portion of the animal kingdom at the upper part of the intestinal canal, and pouring their secreted fluid into it, obviously denotes a connexion between the fluids secreted by these glands, and the changes which the food undergoes in this part of the intestine.

As the function of the pancreas has been determined with greater accuracy than that of the liver, it will be more convenient to consider it first.

Function of the Pancreas in Digestion.—The presence of the pancreas is constant, at least, in the vertebrate classes.

It is present in all the mammalia—it is, perhaps, better developed in carnivora than herbivora; in all it is in intimate relation with the upper part of the small intestine into which it pours its secretion by one or two ducts. In some, as in man, the pancreatic duct and the common choledoch duct open into the duodenum at the same place; in others they open at some distance from each other (as much as sixteen or seventeen inches in the rabbit) but in all they open into the same portion of the intestinal canal; and the pancreatic duct, always *below* the biliary duct, when they do not open together. Some doubt exists as regards its presence in fishes. In rays and sharks a solid gland exists corresponding to the pancreas; and in osseous fishes a similar gland has recently been discovered by Stannius which appears to be its analogue.*

The secretion of the pancreas has some resemblance to saliva. It

* Müller's Archiv., 1849.

has been lately studied with great care by M. Bernard, from whose clear and admirable memoir the following account of it is derived.

The pancreatic fluid may be procured most readily and in greatest quantity at the commencement of the digestive process. Bernard obtained it from the dog in the following manner; the animal having been well fed, after a fast of some hours, an incision was made into the abdomen below the margin of the ribs sufficiently large to enable the operator to draw out the duodenum, and with it a portion of the pancreas. The larger of the two pancreatic ducts was now rapidly isolated, and opened with fine scissors, and into this opening a silver tube was introduced and fixed in the duct by a ligature. The intestine and pancreas were replaced, and the wound in the abdomen closed by suture, the free extremity of the tube being allowed to project through it. To the silver tube was now attached a small caoutchouc bag, perfectly exhausted of air, and to the opposite end of this another similar tube was fixed. The pancreatic fluid flowed freely through the first tube into the caoutchouc bag and accumulated there; and as much as two drachms and a quarter were collected in five hours and a half. The fluid flowed from the tube freely drop by drop.

When this operation was performed at the commencement of digestion, Bernard obtained between half-past seven A.M., and five P.M., four drachms and one third of the fluid, making an average of nearly half a drachm an hour.

On the following day, when signs of inflammation had shown themselves in the wound, more than four drachms of the fluid were obtained in one hour and a quarter. The *quantity* of the secretion was considerably increased, but its *quality* was altered—its consistence being much diminished, and its physiological properties materially changed.

When the experiment was performed on an animal in which the digestive process was fully established, the quantity of fluid obtained was much less than at the earlier period, but its quality much the same. During abstinence only a very small quantity of the pancreatic juice could be obtained at the time of the operation; but the following day, when the wound became inflamed, a fluid much altered in quality flowed out very freely.

If the operation were slowly performed, so as to expose the intestine long to the action of the air, and to irritate it and the gland, the quantity and quality of the secretion were much altered.

As the characters of the pancreatic fluid vary so readily with the circumstances attending the operation of obtaining it, Bernard

describes two kinds of fluid, the first being the *normal*, or that obtained under the best conditions, the second, the *morbid*, or that obtained after inflammation has commenced in the wound and in the pancreas.

The normal pancreatic fluid is a colourless, limpid fluid, viscid and gluey, flowing slowly by large pearly or syrupy drops, and becoming frothy on agitation. It has no characteristic odour—it has a slightly saltish taste resembling that of the serum of the blood. Bernard has always found it *alkaline* in reaction—never either acid or neutral. It coagulates by heat as completely as white of egg, becoming completely solid, and not leaving a drop of fluid. The mineral acids, likewise, cause it to coagulate, as also the metallic salts, alcohol, and pyroxylic spirit. It is not coagulated by dilute acetic, lactic, or hydrochloric acids. Alkalies cause no precipitate in it, but redissolve that thrown down by heat, acids, or alcohol.

This constituent of the pancreatic fluid, which is coagulable by heat, &c., although apparently identical with albumen, is not so: it differs from albumen in the following point. When the coagulum obtained from the pancreatic fluid by alcohol is dried, it can be redissolved completely and readily in water, and it gives to the water the peculiar viscidity of the pancreatic juice, and likewise its physiological properties, whilst albumen treated in the same way, undergoes scarcely any appreciable solution in water.

At a high temperature the pancreatic juice rapidly changes, is decomposed, and loses its property of coagulating by heat. At a low temperature it may be preserved for many days—when its viscidity increases and it becomes of the consistence of a weak jelly. Bernard has examined the pancreatic juice in rabbits, horses, and birds, and has found it in all to exhibit the same essential character as in dogs.

We have already stated that the pancreatic fluid, or a piece of the pancreas itself, is capable of promoting the transformation of starch into sugar, and therefore of promoting the digestion of amylaceous matters. But that this power does not belong exclusively to the pancreatic fluid is evident from the fact that other fluids or animal substances are capable of producing similar transformations. Bernard has shown by direct experiment that the pancreatic fluid possesses the peculiar property, which is not enjoyed by any other animal fluid, of modifying in a special manner or digesting all the neutral fatty matters which are met with in food.

Thus by mixing fresh pancreatic juice, possessing the normal

characters above described of viscidity and alkalinity, with olive oil, and shaking the fluids well together, a perfect emulsion is formed, and a liquid similar to milk or chyle is the result. A similar effect is produced by the admixture of pancreatic juice and fresh butter, or of mutton suet, or hog's lard, care being taken to expose the mixture in a sand-bath to a temperature of from 95° to 100° Fahr., so as to melt the butter and suet, and afterwards to shake the mixture well.

So perfect is the emulsion formed by means of the action of the normal pancreatic fluid upon fatty matters, that the mixture if left from fifteen to eighteen hours at a temperature of from 95° to 100° continues to exhibit the same colour and appearance, nor does any separation take place between the fatty matter and the pancreatic fluid. It appears, nevertheless, that the fat is not simply divided, and made into an emulsion, but that it has undergone a chemical change into glycerine, and a fatty acid; the fluid which immediately after the admixture was distinctly alkaline, becomes, after remaining five or six hours, as distinctly acid. In the tube in which butter had been submitted to the action of the pancreatic juice, butyric acid was easily recognised at a distance by its characteristic odour.

We find that on rubbing up a piece of quite recent pancreas taken from an animal killed during the digestive process, with fat or lard, and a little water at a temperature of 95° or 100°, a very perfect white emulsion is quickly formed.

Bernard instituted experiments to ascertain whether other animal fluids possessed this power over oily or fatty matter. The fluids tried were bile, saliva, gastric juice, serum of blood, and cerebro-spinal fluid, but none of them were found to cause any permanent change, either mechanical or chemical, in the substances submitted to their influence.

It also appears, from Bernard's experiments, and this is a point which may throw some light on certain forms of dyspepsia, that in order that the pancreatic fluid should exercise its perfect action it must be strictly normal. Bernard found that what he calls the *abnormal* fluid, namely, that which exhibits no viscidity, which is watery and does not coagulate by heat, has no effect upon fatty substances.

To complete the proof of the special action of the pancreatic fluid in the digestion of fatty matters, Bernard states that he has tied in the dog the two pancreatic ducts, of which the smaller opens quite close to the choledoch duct, and the larger about three

quarters of an inch lower down. Under such circumstances fat passes through the small intestine unaltered, and the lacteals are filled with limpid chyle totally devoid of the white colour.

The influence of the pancreatic fluid in the formation of the white chyle by its action upon fatty food is beautifully illustrated by Bernard in a very simple experiment upon the rabbit which we have repeated with results precisely corresponding with those obtained by him. The rabbit is selected for this observation, because while the choledoch duct opens into the duodenum just below the pylorus, the pancreatic duct opens as much as sixteen or seventeen inches lower down, so that all that length of intestine receives bile only. A small quantity of melted hog's lard was injected into the stomach, (the animal having been kept without food for twenty-four hours previously) after which it was let to eat freely of parsley and carrots. After five or six hours it was killed. Between the openings of the two ducts the lacteals contained a clear limpid fluid; but *below* the pancreatic duct the lacteals were turgid with a rich white creamy chyle.

In confirmation of these results of experiments it may be stated that patients labouring under disease of the pancreas invariably suffer from extreme emaciation, and many cases are recorded in which fat appeared unaltered in the stools—apparently in consequence of malignant disease of the pancreas. Cases of this kind are recorded by Elliotson, Bright, and others.

From the preceding facts so well collected by the industry and acuteness of Bernard, it seems to us that we must conclude that the principal function of the pancreatic fluid is to digest fatty matters, that is, to reduce them to a state which will admit of their ready absorption by the lacteals. This power is mainly due to the organic principle resembling albumen which is held in solution in the pancreatic fluid.

An objection to this view arises from the fact that some animals have no fat, or oily matter, in their food, as for example many vegetable feeders. This objection, however, may be thus met, that nearly all vegetable substances contain a certain proportion of oily matter, however small—and, moreover, the pancreatic fluid might serve to digest the fatty matters of the bile which by absorption into the lacteals are readily carried to the lungs for combustion.

But that the digestion of fat food is not the *only* office of the pancreas in digestion is sufficiently proved by the experiments of Bouchardat and Sandras already referred to, which point out the important share it takes in the digestion of amylaceous matters.

We may therefore conclude that the pancreas secretes a fluid of which the office is—first and specially to digest fatty and oily elements ; and, secondly, to convert starch into sugar, and thus to promote the digestion and absorption of amylaceous food.

The function of the Liver.—The liver is the largest gland in the body. It is remarkable not only for its complex structure, which will be described in the chapter on Secretion, but also for its peculiar double circulation. It is supplied with blood from two sources, namely, from the *hepatic artery*, which carries red blood to it, and is distributed mainly to the coats of the ducts—and from the *vena portæ*, a vein in structure, but an artery in its mode of branching, which conveys a large quantity of dark blood, derived from the veins of the stomach, the intestines, the pancreas, and the spleen, and which ramifies throughout every part of the liver, passing into a dense capillary plexus, whence it is taken up by the hepatic veins, and carried to the right side of the heart. By this arrangement all matters absorbed into the blood from the gastro-intestinal surface must pass through the liver, a point of anatomy which indicates that the material added to the blood by absorption from the stomach and intestines, in some way contributes to support the function of this gland.

We may justly assume that the bile is secreted from the blood of the vena portæ, because of the great size of that vessel and the vast extent of the capillary plexus, which it supplies, more especially as the small size of the hepatic artery compared with the great bulk of the gland, and the trifling degree to which it can contribute to the formation of the capillary plexus of the organ, clearly disqualify it for contributing to the secreting process.

The bile, as a separated product, first shows itself in the minute canals or ducts which originate in the substance of the liver, and which, by frequent successive junctions, form two large ducts, each somewhat larger than a crow-quill, which emerge at the transverse fissure of the liver, the one from its right, the other from its left lobe. These two ducts pass for a short distance downwards and inwards, enveloped by Glisson's capsule, along with the trunks of the hepatic artery and portal vein, and with the hepatic plexus of nerves and several large lymphatics, with some lymphatic glands. About an inch below their emergence they unite at an acute angle, and form a single duct a little larger than either ; this is the *hepatic* duct, which soon unites with a short duct proceeding from the gall-bladder, the *cystic* duct. The union of these two ducts forms the

ductus communis choledochus, between two and three inches in length, which passes behind the two upper thirds of the duodenum, and opens, along with the pancreatic duct, into that intestine, in or close to the angle of junction of its middle and inferior third.

The gall-bladder is a pyriform bag, placed in a depression on the inferior surface of the right lobe of the liver, and serving as a reservoir for the accumulation of the bile when its flow into the intestine is interrupted or retarded. We infer, at least, that this is its principal use, because it is always found full after a long fast, and empty when digestion is going on. Blondlot tied the common bile-duct of a dog, and established a fistulous communication between the gall-bladder and the external integument; thus the bile, which ought to descend into the intestine, would flow out at this opening. He states that while the animal was fasting sometimes not a drop of bile would escape at the orifice, even for some hours; but in about ten minutes after the introduction of food into the stomach, the bile would begin to flow freely, and continue to do so as long as digestion was going on.* The process of digestion in the duodenum appears to favour the flow of the bile into the intestine either by the stimulus of the food in contact with the mucous membrane acting by reflexion upon the muscular coat of the gall-bladder, and causing it to contract and expel its contents, or, by altering its position, so as to favour the descent of the bile, or by changing the condition of the orifice of the duct, which in the empty state of the bowel would be closed by the contraction of the intestinal circular fibres. Indeed it is probable that all these causes would be brought into operation by the duodenum becoming filled with food, and the digestive process being set up in it.

That the gall-bladder is not an essential part of the excretory apparatus of the liver is shown by the fact that it is not universally present even in the highest classes of animals. This reservoir is found in the animal series first in fishes; but it is absent from many genera of that class. It exists pretty constantly in reptiles and birds, being occasionally wanting in the latter, and in mammalia it is absent from many of the genera. We do not know the precise law which regulates its presence or absence, but it seems that the length of time for which animals are accustomed to fast has probably a good deal of influence. Thus, in the herbivora, which eat often, and at short intervals, and whose digestion is slow, the gall-bladder is frequently absent; and in the carnivora, which eat at long intervals, it is almost constantly present. But

* Essai sur les fonctions du Foie, p. 62.

there are many of the herbivora in which it is present, as in the ox, the sheep, the goat, &c. In the first giraffe examined in this country by Professor Owen there was no gall-bladder; in the second two were found.*

Quantity of Bile secreted.—Various attempts have been made to estimate the quantity of bile secreted by the liver in a given time; but, in truth, we have no satisfactory knowledge on this point. Blondlot, by the experiment upon a dog detailed above, was able to collect the bile that flowed out at the external orifice, which must have been all that was secreted. The quantity thus obtained from one of his dogs amounted in twenty-four hours, on the average, to twelve drams and a half. Assuming, then, with Haller, that the liver of a man secretes four or five times as much bile as that of a dog, we may conclude that the average quantity poured into the human intestine in twenty-four hours is from six to eight ounces. Haller, himself, however, had formed a much larger estimate than this, namely, seventeen to twenty-four ounces.

The Physical and Chemical Properties of Bile.—The bile is a thick, ropy fluid, of a greenish-yellow colour, a bitter taste, and a peculiar nauseous smell, with a specific gravity of 1026 to 1030. It has an antiseptic power, and not only itself resists putrefaction for a considerable period, but prevents substances with which it mixes from putrefying. The excessive fœtor of the fæces in some cases of jaundice from complete obstruction, and, perhaps, also in cholera is probably due to the absence of the antiseptic influence of the bile. The reaction of the bile, according to Gorup-Bezanez, is when first secreted neutral; but subsequently it becomes slightly acid, and ultimately alkaline. The well-known cleansing properties of ox-gall are due to the presence of alkali in it in considerable quantity.

According to the analysis of Berzelius, which seems to be the most trustworthy, and with which that recently made by Mulder† accords very closely, bile consists of water holding mucus in suspension, and in solution certain salts, with a peculiar complex substance called by Berzelius *Bilin*, also fat, and a special colouring matter. The following is Berzelius's table of the analysis of ox-gall.

Water	904·4
Bilin (with fat and colouring matter)	80·0
Mucus	03·0
Salts	12·6
	1000·0

* Art. "Liver," Cyclop. Anat. and Phys.
† Untersuchungen über die Galle, &c. Frankfort. 1847.

According to Berzelius's view of the composition of bile, its essential and most important constituent is the *Bilin*, a substance which has a remarkable tendency, under certain circumstances, to be metamorphosed into taurine, hydrochlorate of ammonia, and into two resinous acids, which he has named *fellinic* acid and *cholinic* acid.

Bilin is inodorous, and has a peculiar sweetish-bitter taste, most perceptible at the base of the tongue and fauces. This sweetness is attributed by Berzelius to the admixture of some glycerin, which may be derived from the fatty matters of the bile. It dissolves readily in water and in alcohol, but not in ether. It is neutral, and forms soluble combinations with acids and bases.

The substances above-named may be obtained from bilin by digesting it in dilute hydrochloric acid. The fellinic and cholinic acids are insoluble, the others are soluble, in water.

Taurin is a crystalline substance, consisting of colourless six-sided prisms. It dissolves in about sixteen times its weight of water at 60°, and is more soluble at a higher temperature. It contains sulphur according to Redtenbacher.* Its composition is represented by the formula $C_4N_2H_4O_6S_2$. The *fellinic* and *cholinic* acids resemble each other very much in their external properties. They are little or not at all soluble in water, but are readily dissolved by alcohol; the *fellinic* acid is readily dissolved by ether, the *cholinic* only slightly. They form nearly similar compounds with the alkalies, earthy and metallic oxides; but their salts of baryta differ; the fellinate of baryta being soluble in alcohol, the cholinate of baryta insoluble. The product called by Berzelius *dyslysin* is obtained by boiling these acids for a long time in hydrochloric acid. It is dissolved with difficulty in boiling alcohol, and on cooling precipitates an earthy powder. *Fellinic* and *cholinic* acids have the property of combining and forming acid compounds with undecomposed bilin; these have been named by Berzelius, *bili-fellinic* and *bili-cholinic* acids.

According to Berzelius and Mulder, bilin begins to undergo these changes in the gall-bladder of the living animal; and it is, probably, this proneness to change on the part of its principal constituent which makes the analysis of bile so difficult, and gives rise to so much diversity of opinion among chemists.

The *fat* of bile exists partly in combination with soda, as oleate and margarate of soda, and principally as a peculiar substance found only in bile and in the nervous matter, namely *cholesterine*. This is separable from the other constituents of the bile by agitation

* Annalen der Chemie und Pharmacie von Liebig und Wohler, Feb., 1846.

in ether, which dissolves it; from this solution it crystallizes in plates. It exhibits, when pure, the white crystalline lamellated structure of spermaceti, from which it differs, however, in requiring a much higher temperature for its fusion, namely 278°, and in not forming a soap with potash. Its formula is $C_{37}H_{32}O$. Cholesterine is the principal constituent of the gall-stones most commonly met with in the biliary passages.

The *colouring-matter of bile* (*cholephyrrhin*, Berzelius) is one of its most interesting constituents. It varies in different animals, and perhaps in the same animal at different times according to the state of health. Like bilin it decomposes very readily, and therefore cannot be obtained pure; but it has been procured for analysis from the gall-bladder, where it is sometimes deposited as a yellow substance mixed with mucus. It is very sparingly soluble in most fluids; scarcely at all in water, and very little in alcohol. Its best solvent is a solution of soda or potass. Such a solution, containing the colouring matter of bile, becomes green on exposure to the air, and on the addition of an acid precipitates green flocculi, which possess all the properties of chlorophyll, the green colouring-matter of plants. To this precipitate Berzelius has given the name *biliverdine*. The most remarkable property of the colouring-matter of bile is the play of colours which it is capable of producing under the influence of a mineral acid, especially nitric acid. A little of this acid, added to bile, or to a fluid in which its colouring-matter is dissolved, as it often is, in urine, will change the colour into blue, green, violet, red, and ultimately brown, in a few seconds. It is highly probable, as some chemists affirm, that there exists a great analogy between the colouring-matter of the bile and that of the blood: as there is also, most likely, between these colouring principles and those of nervous substance, skin, and hair.

In addition to these constituents bile contains *mucus* in considerable quantity, to which probably is due its peculiar viscidity. It is derived chiefly from the numerous mucous follicles in the bile-ducts, and from the mucous membrane of the gall-bladder, and perhaps also from the debris of the hepatic cells after they have burst and yielded up their contents. According to Berzelius the mucus may be separated by filtering the bile, when a considerable portion of it remains on the filter, and if the bile which has passed through be subsequently subjected to the action of alcohol, the remaining mucus will separate; or it may be precipitated by the addition of acetic acid. It is to the presence of this mucus in bile that Berzelius attributes the metamorphic tendency of bilin; and he affirms

that if fresh bile be deprived of its mucus the bilin will continue unchanged for a considerable time.

Among the *saline constituents* of the bile Berzelius enumerates the following:—oleate, margarate, and stearate of soda, with chloride of sodium, sulphate, phosphate and lactate of soda, and phosphate of lime.

Such is the view of the constitution of bile put forward by the celebrated Berzelius, and sanctioned by Mulder. Berzelius remarks that the views which regard bile as a solution of soap, are so far correct, as it contains a small quantity of soap dissolved in it.

The most recent analysis of bile is that by Strecker, made under the direction of Liebig, who denies the accuracy of Berzelius's view, adopting rather that of Demarçay, Dumas, Liebig, and others, that bile is a solution of a salt of soda with an organic substance of an acid nature, which is not a single acid, but a mixture of a nitrogenous acid free from sulphur (*cholic acid*), with a second acid, containing both sulphur and nitrogen (*choleic acid*).

Use of the Bile, and Function of the Liver.—From the anatomy of the biliary organs, as well as from the chemistry of the bile, we learn that, before the venous blood of the intestinal canal and the spleen is allowed to reach the right side of the heart, a fluid very rich in carbon is eliminated from it, and poured into the duodenum. The following questions suggest themselves respecting the uses of this fluid; viz.: is the bile simply an excrement, like the urine? or is it an excrement which also serves some ulterior purpose, such as aiding the solution or digestion of the food in the bowels?

The doctrine that the secretion of bile by the liver, is merely a mode of eliminating carbon from the system, is strongly opposed by the fact that in all the vetrebrate classes the bile, instead of being carried out of the system by the most direct channel, as the urine is, is made to pass through nearly the whole intestinal canal, and to mingle freely with its contents. Moreover, the point at which it enters the bowel always bears a pretty definite relation to that at which the pancreatic fluid is poured into it. Either these fluids enter the bowel together through a common opening, as in man, or the bile is poured in *above*, *never below*, the point of opening of the pancreatic duct.

These are capital facts, which must be accounted for by an adequate theory of the uses of the bile. They indicate that the bile has some use in promoting the changes of the food in the intestines, or in contributing to the general process of nutrition in some other way. It is well known that an obstacle to the free

admission of the bile into the intestinal canal is always followed by a greater or less derangement of digestion, and by more or less emaciation. But, as these consequences might arise not so much from the want of a due admixture of bile with the food which is undergoing digestion, as from the accumulation of the elements of the bile in the blood, which must derange all the functions more or less, Professor Schwann of Louvain tried some experiments which had for their object to stop the flow of bile into the bowel, and at the same time to provide for its excretion. He tied the common bile-duct in dogs, having first established an orifice of communication between the gall-bladder and the skin, through which the bile flowed out of the body as soon as it was secreted, instead of passing into the bowel. It is plain that if the bile were merely excretory, such an operation should produce no injurious effect upon the animal, as still *excretion* was amply provided for.*

Schwann found that of eighteen dogs operated upon in this way two only survived, and in these the divided bile-duct was found re-established, and the bile had resumed its usual channel. Of the remaining sixteen, ten died of the immediate effects of the operation, and the remaining six lingered on for some time, and ultimately died, without exhibiting any other cause for the fatal termination excepting the absence of bile in the intestinal canal. These six died at periods varying from seven days (in a young dog) to two months and a half, the average being two or three weeks after the operation. During this time they exhibited indications of a very enfeebled nutrition, emaciation, muscular weakness, unsteadiness of gait, falling off of the hairs; symptoms which became more developed the longer the dog survived the operation. The emaciation, indicated by a deficiency of weight, began generally on the third day from the operation. When the dogs licked the bile as it flowed out of the fistulous opening, and thus introduced it into the stomach, the digestion in that viscus was not impeded, nor were the results of the operation otherwise embarrassed, showing that it was capable of being digested by the stomach.

Blondlot makes an objection to Schwann's experiments, that, from his mode of operating, the external opening is apt to close, and thus the excretion of the bile is impeded and the nature of the secretion altered. He adopted a different operation, and provided for the free discharge of bile by inserting a canula in the

* Expériences pour constater si la Bile joue dans l'Economie Animale un Rôle essentiel pour la Vie.—Mem. de l'Acad. Roy. de Bruxelles, an. 1844.

wound. A dog, treated in this way, lived three months; at first he became very thin, and lost strength; but he recovered his strength, but did not completely gain his condition. It appears, from a private communication made by Schwann to Frerich,* that that distinguished Professor was induced, by these objections of Blondlot, to repeat his experiments, which he did to the number of thirty, and he took the precaution of keeping a canula in the wound. The animals died as before, but one lived a year, another four months; immediately after the operation they lost weight, but after a time the emaciation ceased, and the dogs recovered, but never reached their weight previous to the operation.

The results of these experiments denote that the bile cannot be exclusively an excretion, and, taken along with the facts already referred to, make strongly against this doctrine. But as the excrements of all, or nearly all animals, and also the meconium, or the feculent matter found in the bowels of the fœtus in utero, contain in certain proportion, the elements of the bile, we are bound to infer, that *a portion* of the bile is thrown out of the system, along with the refuse or undigested parts of the food. And that only *a portion* of it, and that a small one, is thus excreted seems evident, because the quantity of bile contained in the fæces bears a very trifling proportion to the amount secreted. Thus, Berzelius found only 9 parts bile in 1000 parts of fresh human fæces; if we take the average quantity of the fæces expelled in the day to be five ounces, this would yield about twenty-one grains of dried bile, equivalent to 210 grains of fresh bile; but the lowest estimate of the quantity daily secreted by the liver is between six and eight ounces, which exceeds that of the fæces discharged.

If, then, it be admitted that only a certain portion of the bile is excrementitious, it remains to inquire what becomes of the remainder, and what purpose it may serve?

Liebig suggests that it is absorbed from the intestine, and carried into the circulation, where, by chemical union with the oxygen introduced in respiration, it forms carbonic acid, and generates heat. The liver, according to this view, secretes from the venous blood a material, which, on reabsorption, serves as food for the calorifacient process. It is not likely that this absorption takes place by the veins, for if so, we should find the secreted material carried back again through the very same vascular channels from which but a short time previously it had been secreted; an arrangement

* Art. Verdauung, Wagner's Handworterbuch. This author states that Nasse operated on a dog in a similar way, and that the animal lived nearly six months.

which has no parallel in the animal œconomy. It is more probable, assuming this view to be correct, that the portion of the bile absorbed is taken up by the lacteals; and if so, we should have an additional indication that only a part of the bile re-enters the circulation, for if the colouring matter were absorbed by the lacteals it would be readily detected in the chyle.

There are some striking facts which denote a connection between the office of the liver and the calorifacient and respiratory function. Thus, in the boa, although the liver is large, and no doubt secretes bile freely, the excrements contain no trace of bile. In this case, therefore, it must undergo complete decomposition in the intestine, or be entirely absorbed. In carnivorous animals, whose respiratory function is very active, little or no bile is found in the excrements; while in those of the herbivora, which lead less active lives, and whose food is more combustible in its nature, the elements of the bile are present in considerable quantity.

According to this view, the bile would be in part excrementitious and carried off in the fæces; and in part recrementitious, inasmuch as by its absorption into the blood it serves to feed a process highly important to general nutrition, namely, that of animal heat. Still there seem strong grounds for supposing that it must serve yet another purpose; else why should the intestinal blood charged with some of the combustible materials derived by absorption from the digested food be subjected to the action of the liver in order to yield a complex fluid, which is poured into the intestinal canal. In truth, we can find no explanation of this remarkable course of the intestinal venous blood, nor of the situation at which the secreted fluid, the bile, is discharged from the liver, but in the hypothesis that the bile has some function to perform in the intestinal canal.

This leads us to enquire whether the bile has any power of reducing certain elements of food which have been only partially, or not at all dissolved in the stomach.

We have as yet no satisfactory observations which lead to any positive conclusion upon this point. A series of careful experiments as to the influence of bile upon alimentary matters is much needed. Hunefeld's experiments* on this subject tend to establish the general fact that fibrinous and albuminous matters do seem to be dissolved under its influence at a temperature equal, or nearly so, to that of the blood.

The connection of a gall-bladder with the liver in most animals

* Quoted in Valentin, Physiologie, b. i. p. 349.

in which the bile accumulates until intestinal digestion begins, evidently associates the use of the bile with that process.

Sir Benjamin Brodie advocated the doctrine that the bile precipitated the white chyle from the chyme, and was necessary to the formation of the former. He tied the common choledoch duct in young cats so as to prevent the passage of bile into the intestine; and he found that under these circumstances *white* chyle was not formed, the lacteals being filled with a material apparently identical with lymph.* Tiedemann and Gmelin experimented on dogs, and, although they affirm that chyle was formed in the intestine (the accuracy of which statement must not be completely relied upon in default of microscopical examination), yet they admit that the contents of the lacteals in the dog operated on consisted of "a transparent liquid, *not white*," while in the dog not operated on it was white.

By our own experiments we have ascertained that the formation of white chyle took place, notwithstanding the closure of the common bile-duct, provided the animal took a sufficient quantity of *fatty matter* in its food. When this was not attended to white chyle was not obviously formed. But the most remarkable effects of the ligature of the common duct were the emaciation, loss or capriciousness of appetite, and the general debility which immediately ensued upon it. Hence, although we do not subscribe to the doctrine that the presence of bile in the small intestines is essential to the formation of white chyle, we readily believe that its exclusion from the bowels retards and impairs digestion.

When the biliary duct is obstructed, and the bile does not pass through its ordinary channels, the organs which suffer most disturbance in their functions are the kidneys, as if when the liver fails in its action, these organs took on the work of eliminating a certain portion of the bile. They secrete urine loaded with the colouring-matter of the bile; and, at the same time, lithic acid, or lithate of ammonia, or purpurate of ammonia (muroxid), is formed in considerable quantity. In cases of jaundice from obstruction, so long as plenty of bile, or its colouring principle, appears in the urine, and a normal quantity of urine is secreted, no very serious symptoms arise; but as soon as the kidneys fail, then indications of poisoning either by bile or by urea, or both, arise, and the patients die in a comatose state.

It is worthy of remark that the hepatic cells contain more or less of oily fat: and that under some circumstances this fat accumulates

* Quarterly Journal of Science and the Arts, 1823.

in them to a great extent, so as to occasion enormous enlargement of that organ. And in some fishes the liver is naturally, at certain periods, loaded with it. It is a point of great interest to determine, whether this fat simply accumulates in the hepatic cells, as it does in other tissues, or whether it may not be regarded as a part of the secretion of the liver; in other words, can it be a part of the office of the liver to recombine certain elements of the absorbed food, and to form fat, which, on being discharged into the intestinal canal, is absorbed by the villi?*

In connexion with this subject we may refer here to a remarkable fact lately brought to light by Bernard, which denotes that chemical changes take place in the blood while it is passing through the liver, whereby a material is generated in it which had not been introduced in the food.

Bernard has found that sugar is developed in the hepatic capillaries, even when it is not present in the intestines, or in any of the tributary veins of the vena portæ. A dog, which had been fed some hours previously on substances destitute of starch and sugar, was quickly killed, the abdominal cavity was immediately opened, and ligatures were placed on the mesenteric, splenic, and pancreatic veins, and on the trunk of the vena portæ. Blood collected from each of these sources, on the distal side of the ligature, proved on examination destitute of sugar in all, except the vena portæ, in which it was readily detected. Sugar was also found in the tissue of the liver itself. If, then, sugar exists in the vena portæ, but not in its tributary veins, how does it get to the former? As it exists in the tissue of the liver, it is evident that it passes to the vena portæ by the reflux which, in the absence of valves in the portal system, may take place after death. Hence it is reasonable to infer that sugar is formed in the hepatic capillaries, and carried by the hepatic veins to the right side of the heart, in the blood of which Bernard states that sugar is constantly present, whatever food the animal may have been fed on, and even after a long fast.

The evidence of the presence of sugar in the liver is obtained in the following manner:—a portion of the liver is beaten in a mortar, and then boiled in a small quantity of water, and filtered. The filtered liquid possesses all the properties of a saccharine fluid; it becomes darker on being boiled with liquor potassæ, and the

* It is true that the fatty matter of the bile is not free; but it may be supposed to form its combinations after it has been discharged from the hepatic cells, and while it is passing through the ducts of the liver.

addition of the tartrate of potass and copper causes a precipitation of the brown oxide of copper. Yeast added to it at a certain temperature causes fermentation; and alcohol may be obtained from the fermented fluid by distillation.

There can be no doubt, then, that sugar is formed in the capillaries of the liver independently of the food; it is equally certain that fat is separated at the same point, for it appears in the hepatic cells; this, too, is doubtless the result of chemical changes in the hepatic circulation, independent of the food, because we find good grounds for concluding that the fat of the food, emulsified by the pancreatic fluid, is absorbed by the villi, and does not reach the liver.

Thus are formed in the laboratory of the liver these two products —fat and sugar, very nearly allied in chemical constitution. The former is carried into the intestine with the bile, and there absorbed, with the fat of the food, by the villi. The latter is carried by the hepatic veins to the right side of the heart, and thence to the lungs; and both appear to be formed by the liver, whether they have existed in the food or not.

What, then, it may be asked, can be the object of the formation of these products by the liver? If it be to feed the calorifacient process, then the additional question arises, why should each pass to the right side of the heart by a different route?

It seems to us that there is in these arrangements distinct indication of a provision for the *slow* and *gradual* transmission to the lungs of these carbonaceous elements; in order to guard against the blood in these organs becoming surcharged by them so as to interfere with the due introduction of oxygen.

It seems necessary for health that the blood should be supplied, on the one hand, duly, but *gradually*, with carbonaceous matters, such as sugar and fat, and, on the other hand, with oxygen; when the former elements are deficient, fever is the result, the elements of the tissues are consumed by the devouring element, oxygen; and hence it is that we often see such striking results from the gradual introduction of alcohol, or other carbonaceous matters, into the system; but when the latter element is deficient, the great vital changes of the blood are delayed, or suspended, and death rapidly ensues. And in the various diseased states of the body there are infinite shades of difference, as regards the supply or the defect of these great elements; either too much carbon or too much oxygen; or the one is normal in amount, while the other is deficient. A common result of the too ready assimilation of carbonaceous

matters, or the too rapid formation of them, is the deposition of fat in various parts of the body, sometimes to the augmentation of its bulk by an increased developement of the adipose tissue, at others, to the production of various abnormal deposits, containing more or less fat, as atheroma.

In conclusion, the following propositions will serve to exhibit at a glance all that we may, in the present state of our knowledge, affirm respecting the function of the liver:—

1. That it secretes a highly complex fluid, which is poured into the intestinal canal, and there undergoes decomposition. Its colouring-matter (cholephyrrhin, or biliverdin) is carried off in the excrements, and may possibly assist in stimulating the action of the intestine. Its fat is in great part, at least, absorbed by the villi. So much of its fat as is not thus acted upon contributes to form the fæces. Its salts, also, are probably carried off in the fæces. Other of its elements contribute to the digestive process, by promoting the solution in the bowels of some kinds of food which have escaped the solvent action of the gastric fluid. What these elements are, and what kinds of food they serve to dissolve, we have yet accurately to determine; it seems certain, however, that it exercises no solvent power over fatty or oily matters, and probable, that it acts upon azotised matters.

2. The liver forms sugar and fat by chemical processes in its circulation, independently of any direct or immediate supplies of these substances in the aliments.

3. The liver is a great emunctory; it eliminates carbonaceous matters, some directly, as the colouring-matter of the bile, which is at once thrown out in the fæces; others indirectly, as fat and sugar, which, passing to other parts of the circulation, are, more or less acted on by oxygen and eliminated as carbonic acid and water.

4. The liver contributes largely to the maintenance of general nutrition; first, by aiding in the solution of certain aliments in the intestinal canal, and, secondly, by furnishing food to the calorifacient process.

Before we leave this subject, we must refer to the remarkable observations of Weber, confirmed by Kölliker, respecting the extensive generation of blood-corpuscles in the liver of the embryo, which have led the former physiologist to form the opinion that "not only is the liver an organ for secreting bile, but that in it a material is separated and accumulated from the blood, out of which blood-corpuscles are formed, which are taken off by the blood-

vessels, while from the residuum the bile is formed, which is conveyed away by the biliary ducts."

During the latter days of incubation of the hen's egg, the liver assumes a completely yellow colour, instead of the reddish-brown which it had previously. This is connected with the rapid absorption of the yolk, probably by the blood-vessels of the yolk-sac, which carry it to the liver, where it finds its way from the blood-vessels into the fine gall-ducts, which at this time are full of particles exactly the same as the yolk-globules. These particles are not carried into the intestine along the biliary passages, but undergo a change by which, on the one hand, blood-corpuscles are formed and pass into the blood-vessels, and, on the other hand, bile is generated and carried off by the ducts.

Weber states that he has observed a similar phenomenon in the liver of the frog in the spring of the year, when the sexual organs are highly developed, and when the lymphatic system is in a highly active state. The liver undergoes a change of colour from reddish-brown to greenish-yellow. It is covered with dark pigment-cells, and contains numerous opaque masses, which probably consist of the colouring-matter of the bile, which may have accumulated during the winter, but which now undergo gradual solution and pass off in the bile. The peculiar colour which characterizes the liver at this time, in the frog, is resident, as with the chick, neither in the blood-vessels nor in the hepatic cells, but in the minute ramifications of the gall-ducts, which are filled with numerous small globules containing fatty particles. These undergo the same metamorphoses as those of the chick into blood-corpuscles.

This highly interesting subject requires further investigation—to ascertain whether similar phenomena may be noticed in other animals, as in intra-uterine life in Mammalia—or in hybernating animals—or whether, indeed, they may not be constantly occurring in adult animals, although with less activity than in the young.

The question occurs to us, may the liver be a source of supply of blood-corpuscles, or may it contribute to the production of hæmatine in adult life? It has often struck us that this question might be answered in the affirmative, while observing cases in which the process of the formation of blood seemed greatly perverted, where no organic disease could be detected beyond some degree of enlargement of the liver. Patients suffering in this way are pale, as if from loss of blood, although no such loss had been experienced; their nutrition is enfeebled, digestion impaired, and there is slight yellowness of the complexion, as in cases of hepatic

disease, and after death no lesion is discoverable, but slight enlargement of the liver.*

We have already remarked that the venous blood of the spleen passes along with that from the stomach and intestines through the liver. Recent researches of Kölliker and Ecker offer some explanation of this fact, and at the same time of the relation between hœmatine and the colouring matter of bile, as well as between the office of the liver and the generation of the red particles of the blood. It would appear from these researches, which will be detailed when we come to treat of the spleen, that the red blood-corpuscles undergo decay in the red substance of the spleen, giving up their hæmatine in an altered form to the portal blood, from which it may not improbably, as Kölliker conjectures, pass into the bile cells to form, and to be eliminated as, the biliary colouring matter; and, perhaps, also to contribute to supply hæmatine to new blood-cells developed in the liver.†

Of Digestion in the large Intestine.—The contents of the large intestine, which constitute *the fœces* properly so called, differ much from those of the small intestine. Generally, and in the normal state, they are more solid, more homogeneous, exhibiting a certain form, which is determined by the size and shape of the cells of the colon. These characters are more marked the further the fæces have advanced in the colon.

The changes, upon which depends the difference of character of the contents of the large and small intestine, commence in the cœcum. Many facts lead to the opinion that the intestinal contents undergo some further digestion in the cœcum, analogous to that of the stomach. Schulz affirms that an acid fluid is secreted by the mucous membrane of the cœcum, which is more distinct in herbivora than in carnivora; Bernard and Blondlot state that the acidity of this fluid is due to the presence of lactic acid.‡ In dogs, we have found that litmus applied to the surface of the cœcal mucous membrane became reddened in some, but not in others; a difference probably depending upon some peculiarity in the food or the time of digestion. The remarkable developement of the cœcum in some animals as compared with others, denotes that it must exercise some special function. In herbivora its size is especially large; in carnivora, it is small. Moreover, the mucous membrane of the cœcum resembles

* Kölliker über die Blutkorperchen der Menschlichen Embryo und die Entwickelung der Blutkorperchen der Saugethieren.

† Cycl. Anat. and Phys.; art. Spleen.

‡ Gazette Med. de Paris, 1844.

in structure that of the stomach, and is supplied with glands like the solitary glands, which pour out an abundant secretion.

No material change takes place in the fæces as they pass through the large intestine, excepting such as is produced by the absorption of fluid from them by the mucous membrane. Thus the fæces become drier the longer they remain in the bowels.

Defæcation.—The contents of the large intestine are pushed onwards by a vermicular action, essentially the same as that of the small intestine. Propelled thus in successive portions, they accumulate in the rectum, whence they are prevented from escaping by the contraction of the sphincter. The act of expulsion of the fæces from the rectum, the act of defæcation, is effected partly by the contraction of the muscular fibres of the rectum, excited by the stimulus of distension, and partly by the contraction of the abdominal muscles and of the diaphragm, which by reducing the size of the abdominal cavity, and compressing the intestinal canal at all points, greatly assists the detrusive efforts of the rectum itself.

Within certain limits the act of defæcation is favoured by the bulk of the intestinal contents. When the rectum is moderately distended, and its inner surface sufficiently lubricated by mucus, defæcation is effected with but little aid from the abdominal muscles, and mainly by the expulsive force of the rectum, which is sufficiently strong to overcome the passive contraction of the sphincter. If the contents of the rectum be too bulky, they occasion over-distension of the gut, and diminish its contractility. Under such circumstances immense accumulations may take place; and, as small portions may continue from time to time to be expelled, under the influence of the abdominal muscles, the practitioner may thus be deceived as to the real nature of the case. On the other hand, when the fæces do not accumulate in the rectum in sufficient quantity to distend the rectum, the act of defæcation is rendered difficult by the imperfect actions of the rectum itself, and great efforts are required on the part of the abdominal muscles, which often cause the protrusion of portions of the mucous membrane near the anus. Under these circumstances it is that enemata act so favourably, by giving the gut its natural stimulus, that of distension. The action of the abdominal muscles in defæcation is chiefly voluntary, but partly reflex. If the rectum be the seat of irritation, as in dysentery, the reflex action is much increased, and the repeated strainings which occur during the act of defæcation in this disease are, in a great measure, thus caused.

The ordinary expulsive actions of the rectum are due simply to the stimulus of distension acting upon the circular muscular fibres. When the mucous membrane is irritated, as under the influence of a purgative, or in diseased states, the action of the rectum takes on the character of a reflex act, excited by the contact of the fæces with the irritable mucous membrane.

The quantity of the fæces is determined partly by the quantity and quality of the food, partly by the quantity of the secretions poured into the canal. If the food exceed much what the alimentary canal can reduce and absorb, the quantity of fæces will be considerable. Vegetable food produces a greater amount of fæces than animal, because the former is eaten in greater quantity than the latter, and because it contains much that is incapable of reduction in the stomach or bowels. The fæces of carnivora are always absolutely and relatively smaller in quantity than those of herbivora. And those tribes of mankind who feed chiefly on vegetable food make large quantities of fæces.

The ordinary quantity of fæces passed daily by men in health is about five or six ounces; so that, if we assume thirty-five ounces as about the average quantity of food taken in twenty-four hours, it may be inferred that at least thirty ounces are appropriated to the various purposes of the œconomy.

Berzelius's analysis of fæces gives the following result:—

Water			73·3
Matters soluble in water:—	Bile	0·9	5·7
	Albumen	0·9	
	Extractive	2·7	
	Salts	1·2	
Insoluble residue of the food			7·0
Insoluble matters derived from the intestinal canal, as mucus, biliary resin, fat, and a peculiar animal matter			14·0
			100·0

The ashes of human fæces yield according to Berzelius and Enderlin, chloride of sodium, sulphate of soda, tribasic phosphate of soda, phosphate and sulphate of lime, phosphate of magnesia, phosphate of iron, and silica. The nature and quantity of these salts, however, vary with the quality of the food.

A remarkable property of the fæces is their peculiar odour. Upon what this depends has not yet been satisfactorily ascertained. It seems very doubtful that it can depend on any decomposition of the bile; for under certain circumstances, when bile is deficient

or absent, the fetid odour of the discharges from the bowels becomes greatly increased, as in jaundice from obstruction, and Asiatic cholera. It is not improbable that some of the intestinal glands may secrete a peculiar odoriferous principle, which may be modified by the bile. Peyer's glands may perform this office; and this idea derives support from the fact, that in certain cases where these glands are diseased, as in fever and phthisis, the fœtor of the fæces is increased considerably.

Certain gases are generated in the course of the intestinal canal. These are partly set free during the changes which the alimentary matters undergo in the intestine; and partly they are products of secretion from the mucous membrane. They consist of carbonic acid, hydrogen, carburetted and sometimes sulphuretted hydrogen, and nitrogen. A certain quantity of these gases seems, by its distending action, to favour the vermicular movement of the bowels, and so to promote the passage of their contents. Within certain limits, therefore, the formation of gases in the bowels may be presumed to favour health; but, it is well known, that under the influence of emotion, or of irritation, or of certain kinds of food, gases are generated in the stomach, as well as in the intestines, to an enormous extent. Tympanites shows itself in hysteria under the influence of strong emotion; and sometimes a few minutes will suffice to generate a quantity of gas sufficient to distend the whole canal. Also, in fever, the formation of gases in the intestines is a prominent symptom, giving rise to that state of meteorism which is known to be an unfavourable sign in that disease.*

* On the subjects discussed in this chapter the reader is referred to the list of writers at the end of the last chapter, and to those quoted in the foot-notes; also to the following: Berzelius, art. Galle in Wagner's Handworterbuch; Bernard, du Suc Pancreatique, &c., Arch. Gen. de Med., 1849; Bernard, de l'origine du sucre dans l'economie animale, Arch. Gen. de Med. 1848, and translated in Ranking's Abstract for 1849. Frerichs' art. Verdauung, in Wagner's Handworterbuch, a most able essay, which did not reach us until this chapter had been some time in type; Bouchardat and Sandras, Comptes Rendus, 1845; Dr. Allen Thompson's paper on the Intestinal Glands, in Goodsir's Annals of Anatomy and Physiology. Part i. 1850.

CHAPTER XXVI.

OF ABSORPTION. — EXAMPLES. — ANATOMY AND DISTRIBUTION OF THE ABSORBENT VESSELS AND GLANDS.—ORIGIN OF THE ABSORBENTS.—PROOFS OF ABSORPTION.—CONTENTS OF THE ABSORBENTS.—ANALYSIS OF CHYLE AND LYMPH.—THEIR QUANTITY.—MECHANISM OF THE ABSORBENT PROCESS.—THE INFLUENCE OF THE QUALITIES OF THE FLUIDS.—OF THE POROUS SOLIDS.—OF PRESSURE.—OF MOTION OF THE FLUID WITHIN THE VESSELS.—CONCLUDING OBSERVATIONS ON THE FUNCTION OF THE ABSORBENTS.

THE function of absorption is universal in organized bodies, as they all live and grow by absorbing suitable material from without, and making it a part of themselves. All the tissues are more or less porous, and capable of absorbing fluids brought into contact with them. The cuticle of the hands soaked in water become soft and swollen from the imbibition of that fluid, and if a soluble salt be added to the water, this salt may, ere long, be detected in distant parts of the body by its appropriate tests; showing that the foreign substance has penetrated within the cuticle so as to reach vessels capable of diffusing it throughout the frame.* In the same way soluble substances taken into the mouth, and brought into contact with the alimentary mucous membrane, are rapidly absorbed, either immediately, or after having been first changed and adapted for absorption by the processes described in the preceding chapters. In a similar way gases or fluids effused or

* Mr. Erichsen took advantage of a case of extroversion of the bladder to experiment on the rapidity of absorption under different circumstances, as indicated by the presence in the urine of the absorbed substances. The following are some of his results. Prussiate of potass taken into the stomach, after a fast of eleven hours, may be apparent in the urine in one minute; but if immediately after a meal, not till thirty-nine minutes. Vegetable infusions required more time for passage through the system. Galls, uva ursi, madder, rhubarb, logwood, &c., passed in from sixteen to thirty-six minutes, according to the time after a meal. Citrates and tartrates of potass and soda rendered the urine alkaline in from thirty-six to forty-eight minutes. When the *feet were immersed* in a pail of water containing three ounces of acetate of potass in solution, the urine became alkaline in sixty-seven minutes; but no effect seemed to be produced when a solution of citrate, tartrate, or prussiate of potass was employed (see Med. Gazette, June, 1845).

injected into the cavities or interstices of the body may be gradually taken up and removed, as we see in cases of emphysema, of ecchymosis, of dropsy, of inflammatory products, &c. An absorption of the tissues themselves is also constantly going on, as a necessary part of their nutrition—the old materials being taken away when no longer suited for the purposes of life. When the effete matters of the tissues are thrown off from the surface of the body, or from glands, which are, in fact, a portion of that surface, they are said to be secreted; when they re-enter the circulation for a time they may be rightly said to be absorbed. In certain cases, entire organs waste when the term of their usefulness has expired, *e. g.*, the mammary and spermatic glands, and all the organs, even the bones, tend to atrophy in advancing life. Again, periodical absorption of the materials of certain organs occurs, as in the testes of birds and other animals after the annual season of impregnation, but perhaps the most remarkable example of absorption belonging to this head, is that of the fat which is stored up in large quantities in the bodies of hybernating animals, and gradually disappears during the winter torpor, probably to furnish materials for the generation of warmth.

These general observations will suffice to show the importance of the subject of absorption. We are led to it, at the present stage, by having to consider the mode in which the materials introduced into the alimentary cavities are conveyed thence to mingle with and form part of the common mass of the circulating fluid. But we may conveniently treat of the process in general in the present chapter.

The coats of the intestine are found to contain two sets of vessels, one through which blood circulates, from arteries to veins through the capillary network, the other containing a milky or transparent fluid, chyle or lymph, which finally reaches the blood. Both of these kinds of vessels are the agents of absorption, and both probably share in receiving the alimentary matters through the mucous lining of the canal, but in the present chapter the structure of the latter will be chiefly considered, and that of the blood-vessels deferred. Together with the lacteals, the lymphatics will be also described.

The lacteals and lymphatics together form one system of vessels, which takes its rise in the midst of various organs of the body, and conveys a fluid into the veins near their termination in the heart. The lacteals constitute that portion of this great system which originates in the digestive mucous membrane, and they are

undoubtedly concerned in the absorption of a part at least of the nutrient matters of the food—their contents (*chyle*) after a meal being of a milky appearance—whence their name, *vasa lactea,* given to them in 1622 by their discoverer, Asellius. The lymphatics (and the lacteals during fasting) contain a pellucid fluid—the *lymph.*

The *lacteals* originate in the mucous membrane of the intestines, especially in the villi, and form a network with close meshes in the submucous areolar tissue. There are also more superficial ones between the peritoneum and muscular coat, which take a more longitudinal course, and join the others on the mesentery. They then pass in great numbers between the layers of the mesentery towards its root, anastomosing with one another and traversing glandular organs, the *mesenteric glands,* in their way to the right side of the aorta, where they all finally discharge themselves into an elongated pouch common to them and to the lymphatics of the parts below—termed the *receptaculum chyli.* From this the *thoracic duct* leads upwards to the left subclavian vein.

The receptaculum is usually from an inch to an inch and a half in length, and from a quarter to three-eighths of an inch in diameter. The thoracic duct, which is continued upwards from it, lies in the chest between the aorta and vena azygos, then inclines behind the arch of the aorta to the left side, and empties itself into the upper and back part of the left subclavian vein close to the internal jugular vein, its orifice being defended by two valves. The thoracic duct is about an eighth of an inch or more wide, becomes more narrow up to the sixth dorsal vertebra, and again dilates opposite the third. It frequently divides into branches which reunite—and sometimes opens into the subclavian vein by two or even three separate trunks.

The *lymphatic vessels* of the upper and lower extremities form two sets, a deep one accompanying the deep blood-vessels, and a superficial one running in the deeper layer of the superficial fascia. These sets anastomose and pass in common to the trunk by the groin and axilla, where numerous glands occur upon them. (1) Those of the lower extremities after passing under Poupart's ligament, follow the great blood-vessels, are joined by others from the pelvis, loins, and abdominal walls and viscera, and open into the *receptaculum chyli* by from four to six large trunks. Very numerous glands succeed each other in their course, forming an irregular chain. The thoracic duct is joined by lymphatics from the left side of the walls of the chest, and from the heart and left

lung, on all of which many glands occur; and as it empties itself into the great vein, the lymphatics of the left upper extremity, and left side of the head and neck come to meet it. (2) The lymphatics of the right side of the chest, of the right arm, and of the right side of the neck and head, crowd towards the junction of the right subclavian and jugular veins, and open into the former, usually by a large but short trunk. The number of lymphatic glands in the whole body may be estimated at from two to three hundred, or even more.

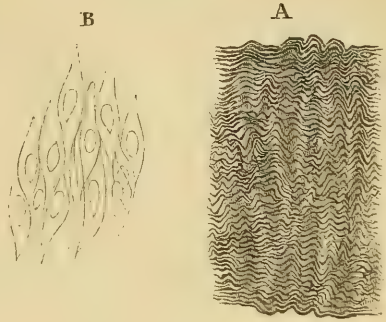
In general, but especially in the limbs, the lymphatic vessels form many trunks of equal diameter, taking the same direction, and joining, and again dividing irregularly, without altering their size. In all this they differ remarkably from the ordinary arrangement of the sanguiferous vessels.

The absorbent vessels differ from the blood-vessels in the delicacy and semi-transparency of their coats, which allow the nature of the contents to be seen through them; the white colour of the chyle in the lacteals, or mercury artificially thrown in, is at once visible from the outside. When the vessels are filled we observe many constrictions, depending on the existence of valves in the interior, so placed as to prevent a retrograde flow of the chyle or lymph. These valves are closer together in some parts than in others. In general they are further apart in the narrower vessels, but in the thoracic duct, the largest of all, they are unfrequent. They are usually closest set in vessels of medium size, *i. e.*, in those of from $\frac{1}{12}$th to $\frac{1}{16}$th of an inch diameter, but they are not so near to one another in the lymphatics of the upper extremities, and the head and neck, as in those of the lower limbs. Besides occurring in succession in the course of the vessels, they are almost always found at the origin or termination of branches, and also where the lymphatics empty themselves into the veins.

The absorbent vessels have a proper coat, an outer investment of areolar tissue, and an inner lining of epithelium. (1) The proper coat is formed chiefly of circular fibres, relatively most abundant in the smaller vessels, analogous to the contractile tissue of the blood-vessels, and a modification of the unstriped muscle, containing elongated nuclei. On the inner side of the circular fibres are longitudinal fibres, more resembling white fibrous tissue (fig. 169, A). (2) The fibres of the areolar coat have an irregular course, and blend with the neighbouring tissues. This coat allows of slight movements of the vessel, and contains the blood-vessels which ramify in considerable abundance on the proper coat. (3) The epithelial lining consists

of a single layer of extremely delicate nucleated particles, first noticed by Henle. They are usually spindle-shaped, and fitted side-ways to each other (fig. 169 B).

Fig. 169.



A. Longitudinal wavy fibres on the inner surface of the contractile transverse fibres of the thoracic duct of the horse. —Magnified 80 diameters.
B. Stratum of nucleated epithelial cells lining the lymphatic vessels.—From a large lymphatic on the trachea of a horse. Magnified 320 diameters.

The valves (fig. 170 C) are formed by a process of fibrous membrane standing off into the vessel, probably with a covering of the epithelium. They are mostly in pairs, of a crescentic shape, the convex edge attached, the concave free, and when in action constitute a perfect barrier, the wall of the vessels immediately above them being bulged into a sinus, so as to give the canal a beaded appearance when distended. Mr. Lane has observed that some of the valves are single and circular, with a central perforation, and therefore incomplete — while others are unequal in size.

Fig. 170.

A. One of the inguinal lymphatic glands injected with mercury. *a.* Afferent lymphatic vessel from the lower extremity. *b.* Efferent vessel. Others are also seen.
B. One of the superficial lymphatic trunks of the thigh.
C. One of the femoral lymphatic trunks, laid open longitudinally to display the valves within it. *c.* Sinus between the valve and the wall of the vessel. *d.* Surface of one valve, directed towards the opposite. *e.* Semicircular attached margin of the valve. After Mascagni.

Contractility of the absorbent vessels. — This depends on the contractile tissue of their proper coat. The property may be demonstrated by mechanically irritating a large vessel, such as the thoracic duct, in an animal just killed — it undergoes slow contraction. The absorbent vessels continue to propel their contents, even when the current from the primary networks is arrested by pressure, and this they

seem to do by their vital contractility. As the contents advance the vessels diminish in diameter. It is usual to find the lymphatics empty and collapsed some time after death.

The *lymphatic glands* are, for the most part, flattish oval bodies, of firm consistence and light colour, situated in the course of the lymphatic and lacteal vessels, these vessels being styled afferent as they enter the gland, and efferent as they leave it. The glands vary from the size of a millet-seed to that of an almond. They usually lie loosely in the areolar texture, well protected from injury by their mobility, and if near the surface of the body, by the disposition of the neighbouring bones or muscles. They have a firm but delicate proper capsule, which is continuous with the outer coat of the vessels, and which sends processes inwards upon the bloodvessels and lymphatics which penetrate the glands.

The general structure of these glands has long been known, being well displayed by mercurial injections (fig. 170, A). This metal, when thrown into an afferent vessel, shows that this divides into minute branches, most of which spread out over the gland before entering it, and that the efferent vessels have a similar arrangement on the opposite side. The mercury readily fills the entire gland, and escapes by the efferent vessels. The surface of the gland, when occupied by mercury, exhibits either a very close plexus of tortuous minute vessels, or else a congeries of apparent cells; and while there has been no doubt of the continuity of the internal tracts of the gland with both the afferent and efferent vessels, the question has been discussed, whether these tracts are simply convolutions of tubes, or cellular lateral offsets from channels traversing the gland in a more direct course. Both of these views may possibly be true in different cases, or probably the convoluted vessels of the gland may be themselves dilated at intervals into cells which, from their mode of package, may simulate detached cavities, as in the well known arrangement of the vesiculæ seminales. In confirmation of this last view it may be observed, that the tracts of the gland are usually more capacious than the ramifications of the afferent and efferent vessels which immediately communicate with them.

A more important question concerns the changes in the tissues forming the walls of the afferent vessels on their entrance into the gland, and this has been ably illustrated by Professor Goodsir. He describes the outer areolar coat as passing to form the capsule of the gland, and the proper coat to become extremely thin, especially

in the deeper parts of the gland. The epithelium, however, becomes thicker and more opaque, so as often no longer to transmit the light under the microscope, and by the action of acetic acid very numerous nuclei are disclosed in it. He describes the elongated nuclei in the substance of the (proper) membrane on which this modified glandular epithelium rests, and appears to consider that the epithelium is in constant decay and renovation, being shed as a secretion into the cavity of the ducts, to mingle with and modify the passing lymph.*

From the examinations we have made of the recent glands of the lower mammalia, we are disposed to agree in most particulars with this description. The very delicate simple layer of transparent nucleated cells lining the lymphatic vessel ere it enters the gland, becomes in the gland a very thick and rather opaque granular mass loaded with nuclei, in the debris of which are apparent a great abundance of nucleated cells of different sizes, many of them precisely resembling the white or colourless lymph corpuscles presently to be described. We lean strongly to the opinion that these corpuscles are set free to a large amount, though, perhaps, not exclusively, from the surface of the intra-glandular passages. The structure of the lymphatic glands offers many difficulties to the anatomist, and there can be little doubt that further research would discover peculiarities as yet undetected.

The lymphatic glands are well supplied with blood. The arteries and veins derived from neighbouring sources subdivide together on the surface, and penetrate between the ducts, carrying in with them for some distance a sheath derived from the capsule. The capillary network is probably spread out on the exterior of the ducts, *i. e.* in the interstices of the plexus which these form in the gland; but it cannot be said that the exact relation of the blood-vessels to the abundant granular matter of the ducts has been as yet unequivocally demonstrated. The capillaries are very fine, their meshes large, and they anastomose throughout.

In injections of the ducts of the glands, the mercury is found to find its way very readily into the veins, but not into the arteries; and it has been concluded by Fohmann, that this indicates a natural communication between these sets of vessels in the glands. This view is certainly rendered plausible by the proved termination of the lymphatics in the veins of the neck, and by the fact which appears to be established by the observations of Fohmann, Lauth,

* Anatomical and Pathological Observations.

and Panizza, that in birds, as well as in reptiles and fishes, there are communications with the small veins at many points of the pelvis and abdomen. Nevertheless, the evidence for such a communication in the lymphatic glands is very unsatisfactory. The more probable explanation of the fact above noticed seems to be, that the brittle texture of the interior of the glands readily gives way before mercury, and that then the minute veins, which are more numerous than the arteries and less resisting, are the first to receive the extravasated metal.

Origin of the Lymphatics.—We have before spoken of the origin of the lacteals in the villi of the small intestines. The lymphatics in other regions have been usually considered to arise in the substance of the skin and mucous membranes, and on the surface of the viscera by a plexus of somewhat variable character. In the skin and elsewhere the meshes are very close and small, while on the lungs they are much more open and the vessels larger. The surface of the liver and spleen is overrun with

Fig. 171.

Part of a ramification of a lymphatic of the under part of the tail of a tadpole. *a*. Simple membrane, forming the wall of the vessel. *b*. Prolongation or process of this membrane. *c*, *d*. Fatty granules attached to the inner surface of the membrane, and surrounding the nuclei. *e*. A closed extremity of the vessel. *f*. Branched cell, just united to a corresponding extremity. *g*. Branched cell, on the point of coalescing with a capillary lymphatic vessel already formed.—Magnified 400 diameters. After Kölliker.

a network of lymphatics of remarkable luxuriance. So far as mercurial injection can inform us, these plexuses are the commencement of the lymphatic system; but we have been recently made acquainted with a system of lymphatic vessels discovered by Kölliker in the tail of the larvæ of batrachian reptiles, which renders it probable that a still finer series exists in the higher

animals and in man, than those comparatively large ones which compose the plexuses just mentioned, Kölliker observed these vessels during life, and satisfied himself of their continuity with the neighbouring lymphatic trunks. He found them about the same size, but less numerous than the blood-capillaries, and composed of a simple, very delicate membranous wall, projecting into small pointed processes, here and there, and containing a few flattened nuclei. The pointed processes may belong only to their rudimentary, and not to their completely developed condition. He states that they ramify in an arborescent manner, without anastomosing, and end by free closed extremities. They have no valves, and remain of the same width during life, but after death, exhibit the same contractility, though not of so active a kind, as the capillaries, by lessening uniformly in diameter during a certain time. He was able to detect the movement of their transparent contents by that of the granules and lymph-corpuscles which, in rare instances, they were observed to contain, and found it to be continuous, and very slow, almost twelve times as slow as that of the blood in the capillaries. He found the mode of developement of these primary lymphatics to resemble closely that of the capillaries, *i. e.*, it takes place by the outgrowth and subsequent coalescence and tubulation of processes from contiguous nucleated cells.

Kölliker's observations on the relations of these minute lymphatics with the capillaries are interesting. He found that when the current of blood was regular, there was no appearance of communication between the two orders of vessels, but that when the circulation was excited and tumultuous, owing to the confinement of the tadpole under glass, during the observation under a high magnifying power, red blood-corpuscles escaped more or less readily from the blood-vessels into the contiguous lymphatics; and in several instances he was able to detect actual communications between lymphatics of the finest kind and the network of capillary blood-vessels. After careful inquiry, however, he concludes that these junctions are due to rupture, or, perhaps, in some cases to a primitive abnormal formation. He further noticed a reflux of blood into the lymphatics through the orifices by which their trunks open into the larger veins. This retrograde current was almost always observed when the respiration was impeded by want of water, and the veins were consequently gorged, or when a ligature was placed round the head. In the latter case, the whole lymphatic tree was often fully and beautifully injected with blood.

A lymphatic system exists in all the vertebrata, but the glands are wanting in fishes and reptiles, and are very few in birds, being found only in the neck. In fishes and reptiles, however, there occur large and intricate lymphatic plexuses, chiefly without valves, accompanying and sometimes completely surrounding the blood-vessels in a luxuriance quite superior to anything found in the higher classes. Moreover, there exist in the course of the lymphatic trunks in these animals and in birds, pouches furnished with valves and muscular walls, which contract rhythmically and urge on the lymph towards the veins. These *lymphatic hearts* are, in birds at least, formed of the striped fibre, according to the observation of Stannius; and we owe to Volkmann the interesting fact, that in frogs their contraction may be excited by the direct influence of portions of the spinal marrow.*

Do the Lacteal and Lymphatic Vessels absorb? — From the account now given it is clear that the structure and arrangement of the lymphatic vessels fit them only for the conveyance of fluid in one direction, viz., from the various tissues in which they originate to the great veins, and thence to the heart. Hence there can be no doubt, that, whatever other function they may subserve, they are designed to carry fluid into the blood either from the exterior of the body, as in the case of the digestive mucous membrane and the skin, or from the interstices of the various textures, where it may have been derived either directly from the circulating mass, or indirectly from the waste of the textures themselves. It was till lately assumed too exclusively that this system of vessels was the sole agent in such absorption, and hence the name of absorbent system as applied to it, and the view which allowed the blood vessels no share in the absorbent function.

To prove that the lacteals absorb chyle, it is only necessary to examine them in a fasting and in a recently fed animal. In the former their contents are transparent, in the latter they are milky, and the opaque fluid can be shown by simple means to move on in the course indicated by the valves. That the lymphatics absorb is perhaps best shown by the phenomena of disease. The syphilitic poison is frequently carried from the primary sore along the lymphatics, and exciting inflammation in this route may occasion deposits of lymph or pus either on the penis or in the groin, and the matter of abscesses so formed is capable of imparting the disease to other individuals, thus proving the multiplication, and, probably, also the real transport of the virus along these channels. The inflammation of the lymphatic trunks and glands so often observed to ensue upon accidental wounds, either poisoned or not, especially in debilitated subjects, seems due to an actual propaga-

* Paget's Report, 1844—5, p. 27.

tion of morbid materials in the current of the lymph, exciting inflammation in successive parts as it comes into contact with them; and the severe constitutional disturbance usually attendant on this state of lymphatic inflammation is attributable, with a high degree of probability, to a discharge of some such morbid fluid contaminating the lymph into the blood-vessels, so as to mingle with the general circulating mass of blood. Wagner mentions that the axillary glands of a subject brought for dissection were found of an intense red colour from the deposition of cinnabar in their texture, while on the arm was a red tattooed figure of old date, which had evidently furnished the material.*

That the blood vessels also absorb, however, is rendered certain, not merely by considering that their structure and physical conditions furnish every element requisite for this function, but by experiments of a conclusive nature. Panizza poisoned a horse, by confining hydrocyanic acid in a loop of intestine, which was separated from the body excepting by one artery and vein which maintained the circulation in it. As long as the vein was compressed the animal escaped, but when the pressure was remitted the poison took effect; and in blood drawn from the vein the acid was detected.

Contents of the Absorbents.—The lymphatics (and the lacteals when digestion is not going on) contain a nearly colourless and transparent fluid, termed lymph, in which are included a number of colourless nucleated cells of globular shape (*lymph corpuscles, colourless corpuscles*) analogous to, and even identical with, the colourless corpuscles of the blood. The lacteals during the digestion of fatty matters always contain another element which gives a milky hue to the chyle, viz. a finely granular matter, termed by Mr. Gulliver the *molecular base.*

Lymph and chyle, when withdrawn from their vessels, spontaneously coagulate into a slightly coherent jelly in the course of a few minutes. This property depends on the presence of fibrine in a fluid form, as in the blood, and varies with the point from which the lymph is drawn, as well as with the activity of the nutritive vigour in the animal at the time. The clot at first entangles the floating particles, and if the fibrine have sufficient energy, it undergoes some degree of subsequent contraction, by which a loose mesh is separated from the fluid part, as the crassamentum from the serum of the blood. Most of the corpuscles usually remain in the clot, though some escape and remain with

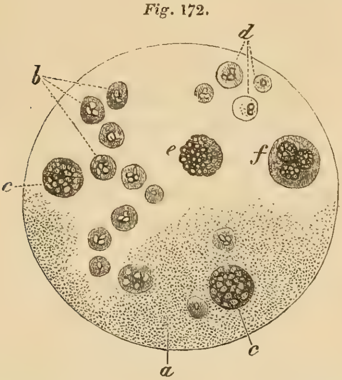
* Physiology, by Willis, p. 440.

the fluid element. The coagulability of the lymph appears to bear a close relation to that of the blood in the same animal.

Lymph.—The liquid portion, *liquor lymphæ*, is supposed by some to be simply albuminous in the primary network, and to acquire its fibrine on its passage onwards through the vessels and glands towards the veins. The fibrine is found in increasing quantity towards the main trunks, though never in so large a proportion as in the *liquor sanguinis*. The same kind of saline matters are also met with in the liquor lymphæ as in the liquor sanguinis, together with a trace of fatty substance and some iron.

The *lymph corpuscles* are very scanty in the primary network and branches (as already noticed in the observations of Kölliker), and they increase in number, and perhaps in size, towards the trunks, especially as they pass the glands. They present themselves under some varieties; in one, and this is the most usual, the nucleus is concealed by a granular matter, in another this granular matter appears in process of removal or deliquescence, so that the nucleus is visible—or, again, the interval between the nucleus and the cell-wall may be quite clear, and the granular matter wanting. These corpuscles are called by Mr. W. Jones respectively the *granule-cell* and the *nucleated cell in the uncoloured stage*, and he further points out that there are in the lymph other nucleated cells approximating in colour to the red-corpuscles of the blood, and which he regards as in progress to become red blood corpuscles, by losing their cell-wall, and becoming reduced to a simple nucleus.*

Fig. 172.



Fluid from a mesenteric gland of a rabbit, when white chyle was present in the lacteals. *a*. Molecular base. *b, c, d.*, &c. Various organic corpuscles. *b*. Appearance of the majority of corpuscles. The contained granules are most numerous and coarse in the largest ones, but almost entirely disappear under the action of acetic acid, which thereby discloses an appearance of one or two nuclei. The majority of the corpuscles are either large or small, and but few of intermediate size. *d*. Exhibits the effect of acetic acid in rendering the corpuscles more clear and their nuclei more distinct. *e*. Large lymph-corpuscle, showing well the granulated border. *f*. Large corpuscle, apparently inclosing three smaller ones, each of which has the granulated character. This appearance of inclosed cells is not common.—Magnified 300 diameters.

Besides these true corpuscles of the lymph, it is very common to

* Philosophical Transactions, 1846, p. 82, and the next chapter, on the Blood.

find in it red blood-corpuscles. These, it is probable, have been accidentally introduced into the lymphatic vessel during the dissection employed to lay it open.

Chyle.—The *liquor chyli* contains more albumen, and more fat than the liquor lymphæ. It has been noticed that the lacteals near the intestine contain little or no fibrine; their contents do not acquire the power of spontaneously coagulating till we approach the main trunks. Even in the receptaculum chyli and the thoracic duct, where the chyle is commingled with the lymph from distant parts, the clot formed is still much softer than that of blood.

The corpuscles of the chyle are the same as those of lymph. In addition, however, we have in most instances the *molecular base.* This varies with the amount of fatty matter in the food. It gives the chyle that milky colour which was shewn by Tiedemann and Gmelin to have a close correspondence with the fat of the food. It has been noticed to be generally absent or very deficient in birds; it is less abundant in herbivorous animals than in carnivorous. If a dog be fed on food, from which fat is carefully excluded, the chyle is not milky, but whey-like or transparent.

Sir Benjamin Brodie, in 1816, fed a cat on jelly, and a dog on isinglass jelly: the animals were killed after two hours. The stomachs were found nearly empty, the duodena filled with a mixture apparently of chyle and jelly; the lacteals and thoracic ducts contained *transparent chyle*, which coagulated spontaneously. He likewise fed a dog on lard, after a fast of thirty-six hours, and in three hours killed the animal. Some lard was found in the stomach, some fluid of albuminous character in the duodenum, the same tinged with bile in the ileum, and in the thoracic duct perfect *milky chyle.**

The molecular base is present in the lacteals from the very commencement, even from the villi of the intestines. It seems to consist of almost infinitely small particles (*fig.* 172 *a*) of oleaginous or fatty matter, thrown into this form by contact with the pancreatic secretion, as so well proved by Bernard. The particles do not look like oil under the microscope—their outline is not definite or sharp, and from this circumstance, as well as from their extreme minuteness, it is not easy to assign them an exact size. In fact, they vary somewhat. Mr. Gulliver makes their diameter $\frac{1}{30000}$th of an inch. Thus the white colour of the chyle does not depend on precisely the same cause as that of the milk, for the

* "Selections from Notes of Physiological Experiments," by Sir B. C. Brodie Bart., MS. pp. 39, 40, 41.

latter exhibits under the microscope myriads of true oil-globules of different sizes. A few oil-globules are commonly found in the chyle, but they are probably extraneous.

Dr. G. O. Rees gives the following analysis of the contents of the thoracic duct of a criminal, who had taken two ounces of bread and four ounces of meat on the preceding evening, and two cups of tea and a piece of toast an hour before he was executed, and whose body was examined one hour and a quarter after death. Nearly six drachms were obtained, of a milky hue, with a slight tinge of buff.*

Water	90·48
Albumen, with traces of fibrine	7·08
Aqueous extractive	0·56
Alcoholic extractive, or Osmazome	0·52
Alkaline chloride, carbonate, and sulphate, with traces of alkaline phosphate, and oxide of iron	0·44
Fatty matters	0·92
	100·00

The following is his analysis of the lymph and chyle of the ass:†—

	Lymph.	Chyle.
Water	96·536	90 237
Albumen	1·200	3·516
Fibrine	0·120	0·370
Extractive	1·559	1·565
Fatty matter	a trace	3·601
Salts	0·585	0·711
	100·000	100·000

These latter may probably be taken as fair samples of the constitution of the lymph and chyle. Much variety, however, will of course exist in specimens, derived from different animals, and at different periods of digestion. The chief distinctions between lymph and blood, are—1st. The absence of the red particles in the former, and, 2nd. The smaller proportion of albumen and fibrine. Chyle differs from blood in the same points, and, moreover, in its large proportion of fat, which may rise, according to Nasse, as high as 15 in 1000. Chyle differs from lymph in containing more albumen, and much more fat.

Quantity of chyle and lymph.—That the chyle enters the blood very rapidly along the lacteals during digestion is obvious on opening the body of an animal. It is easy to collect from the

* Phil. Trans. 1842, p. 82. † Med. Gazette, Jan. 1841.

thoracic duct of a small dog, in the course of a few minutes, as much as will fill a watch-glass. If absorption is actively going on at the moment, a ligature on the duct will often be followed by a rupture of some vessel below by the onward pressure of the current. So the lymph, in some instances, has been collected in considerable quantity in a short space of time. Geiger, from an open lymphatic on the foot of a horse, collected from three to five pounds of lymph daily. Bidder has performed some experiments on cats, from which he estimates that a quantity of lymph and chyle, together equal to one-sixth the weight of the body, or the whole weight of the blood, enters the circulation every twenty-four hours. But it must be borne in mind that this does not all form new supply, the lymph being, probably, in large measure derived from that liquor sanguinis which has escaped from the capillaries into the interstices of the tissues, and which cannot re-enter the capillaries in a direct manner.

Mechanism of Absorption.—In considering this part of the subject the following points should be remembered :—

1. The process of absorption in living bodies implies *imbibition* by their tissues and subsequent *transmission* of the imbibed fluid by the vascular channels to distant parts.

2. As regards imbibition, it is a phenomenon of a purely physico-chemical nature, and occurs in inorganic as well as organic bodies, and in organic bodies both when dead and living. It depends mainly on the force of adhesion between a fluid and a porous solid, by which the fluid is drawn into the interstitial passages of the solid.

3. The fluid chiefly concerned in this process in all animal and vegetable bodies is water, which, as already stated, has a close affinity for their tissues and forms an essential ingredient of them, without which they, for the most part, lose their vital and physical properties.

4. The various other substances which are imbibed in living bodies are taken up in a state of aqueous solution, such as gases, albumen, fibrine, salts, &c.

5. Where the fluid is rendered complex by holding in solution various substances which have different degrees of the force of heterogeneous adhesion for each other, for the water they are dissolved in and for the porous solid, the phenomena of their transmission are also complex : various preferences, if we may so express it, exist ; one ingredient penetrates rather than another, and the results depend very much on the chemical qualities of the elements concerned.

6. The laws relating to the mixture of different fluids also exert an important influence on the phenomenon.

Referring to a former page (vol. i. p. 53) for a brief notice of the phenomena of endosmose and exosmose, as observed by Dutrochet, we may conveniently proceed with the consideration of the mechanism of absorption in the living body under the following heads.

Absorption, as influenced by the Qualities of the Fluids.—It was

shown by Chevreul, that an animal tissue imbibed very different amounts of different fluids with which it was brought into contact after it had been dried. Thus the cornea took up water, brine and oil, in the proportions of 461, 370 and 9; and Liebig, in experiments with the dried bladder of the ox and pig, has found that "of all liquids, pure water is taken up in the largest quantity; that the absorptive power for solution of salt diminishes in a certain ratio as the proportion of salt increases; and that a mixture of alcohol and water is taken up more abundantly the less alcohol it contains."*

The mixture of two dissimilar fluids through a membrane is much influenced by their respective attractions for the membrane. Thus, as water has a stronger affinity for the membrane, than brine or alcohol, it permeates it more readily and arrives in greater quantity in a given time on the opposite surface than either of those fluids. Hence more water comes through to mix with the alcohol, than alcohol to mix with the water, and an accumulation of the mixed fluids consequently takes place on the side of the alcohol: for the alcohol, or the water, having once traversed the thickness of the membrane, comes into contact with the opposite fluid, and becomes diffused through it in obedience to known laws. The same is true in regard to various substances miscible with water or dissolved in it.

Within the blood-vessels and the lymphatics is a fluid considerably denser than water, and having less affinity for the walls than water. Hence, if water be applied to the surface of the body or taken into the stomach, it readily enters the circulation, particularly in the latter case, where it is brought into much closer contact with the blood-vessels. If a quart of warm water be injected into a torpid colon, half an hour will almost suffice to convey it into the blood-vessels, and thence through the kidneys into the bladder. If, however, the injected water hold a considerable quantity of common salt in solution, it will be absorbed more slowly; while, if the solution be a concentrated one, the fluid portion of the blood will pass out of the vessels to mix with the saline solution. The action of many medicines taken by the mouth, particularly of saline purgatives, is in some measure explained by these laws.

It is interesting to notice that albumen passes less readily through an animal membrane than gelatine, gum, or sugar. Thus alcohol,

* Researches on the Motion of the Juices in the Animal Body. Translated by Wm. Gregory, M.D. London: 1848. P. 9.

ether, oil, albumen, gum and sugar would disappear from the stomach in very different intervals of time.

Absorption as influenced by the Porous Solid.—An extensive and accurate series of experiments has been recently performed by MM. Matteucci and Cima, in which they investigated the influence of different kinds of animal membranes, and of various arrangements of them, on the transmission of various fluids. They employed—1. The skin of the frog, the torpedo, and the eel; 2. The mucous lining of the stomach of the lamb, cat, and dog, and of the gizzard of the fowl; and, 3. The mucous lining of the bladder of the ox and pig. The following are the general conclusions derived from these experiments, in the words of their translator:—

"1st. The membrane interposed between the two liquids is very actively concerned, according to its nature, in the intensity and direction of the endosmotic current.

"2ndly. There is, in general, for each membrane a certain position in which endosmose is most intense; and the cases are very rare in which, with fresh membrane, endosmose takes place equally, whatever be the relative position of the membrane to the two liquids.

"3rdly. The direction which is most favourable to endosmose through skins, is usually from the internal to the external surface, with the exception of the skin of the frog, in which endosmose, in the single case of water and alcohol, is promoted from the external to the internal surface.

"4thly. The direction favourable to endosmose through stomachs and urinary bladders varies with different liquids, much more than through skins.

"5thly. The phenomenon of endosmose is intimately connected with the physiological (natural or healthy) condition of the membranes.

"6thly. With membranes, dried or altered by putrefaction, either we do not observe the usual difference arising from the position of their surfaces, or endosmose no longer takes place."*

With the mucous lining of the stomach of the lamb (whether the paunch or the true digestive stomach is not mentioned) these trustworthy experimenters found that water passed through towards a solution of sugar in greater quantity when the water was at first placed on that side of the membrane which is naturally turned towards the interior of the cavity of the stomach, than when it

* Lectures on the Physical Phenomena of Living Beings. By Carlo Matteucci. Translated under the superintendence of Dr. Pereira. London: 1847. P. 65.

was placed on the opposite side; the proportions being about as six to five. On the contrary, when solution of white of egg was used, water passed more readily, when placed in contact with the attached or submucous surface than when in contact with the free or epithelial surface. It passed also towards the albumen in only half the quantity that it did to the sugar. Again, with a solution of gum, the endosmose was very feeble, whichever way the membrane was turned—and seemed to follow no rule.

These facts show the influence exerted by the structure or chemical properties of the membrane in this process, but we are still very much in the dark as to the intimate cause of the influence thus operating.

They are sufficient, however, to indicate the extremely important principle in physiology, that the chemical and structural properties of the tissues exert a great influence on all those processes in which the molecular motion of fluids is concerned.

The thickness or thinness of the membrane also much affects the result, and that for an obvious mechanical reason. If the transmission of fluids is so rapidly carried on out of the body, through the entire thickness of compound and dense membranes, how much more expeditious must it be in the living tissues, where the external fluid has in general but one or two very attenuated films of membrane to traverse in order to arrive within the capillary blood-vessels.

Absorption as influenced by Pressure.—The influence of pressure on the passage of fluids through membranes is illustrated by a common filter, or by tying a membrane over one end of a vessel containing fluid, to which a syringe capable of applying various degrees of pressure is adapted. In the latter case, the rapidity of transmission will be found, *cæteris paribus*, to depend on the degree of pressure employed, and after a certain time the transmission will be accelerated by the enlargement of the pores of the membrane. In this way pressure may be used as a test of the relative transmissibility of different fluids through membranes of various thickness and quality, and Liebig has found that "through ox-bladder, $\frac{1}{120}$th of an inch thick, water flows under a pressure of twelve inches of mercury; that a saturated solution of sea salt requires from eighteen to twenty inches; and that marrow oil only flows out under a pressure of thirty-four inches of mercury.

"When the membrane used is the peritoneum of the ox, $\frac{1}{240}$th of an inch in thickness, water is forced through it by eight to ten inches, brine by twelve to sixteen inches, oil by twenty-two to

twenty-four inches, and alcohol by thirty-six to forty inches of mercury:" and hence it appears, as this eminent writer remarks, that "the power of a liquid to filter through an animal membrane bears no relation to the mobility of its particles; for under a pressure which causes water, brine, or oil, to pass through, the far more mobile alcohol does not pass."

As pressure promotes the transmission of fluid through a membrane in one direction, so it tends to interrupt the passage of the other fluid in the opposite direction,—or to apply this to the blood-vessels of the living body, if they are distended by an over great quantity of blood, so that this fluid reacts upon their inner surface, as in the case of plethora, fluids enter them with difficulty from without—whereas, if their bulk is diminished by venæsection, absorption is comparatively rapid. This conclusion was established by Magendie on good grounds, and it has some illustrations and valuable applications in practice.

Absorption as influenced by motion of the Fluid within the Vessels.—Fluid may be raised out of a reservoir against gravity, by directing a stream along a membranous canal, which lies immersed in the stagnant fluid. The outer fluid enters the canal by endosmose, and is carried away with a speed proportioned to the velocity of the current. If the fluid in motion is so compressed as to exert much lateral pressure on the wall of the tube, it will rather itself pass outwards, so as to mingle with the fluid at rest, than receive and carry off the latter. If the fluid in motion is also the more dense, or otherwise that towards which the external fluid would flow if both were stagnant, then its motion accelerates the endosmose by constantly bringing on fresh fluid of the original density, so that the first rate of transmission is maintained.*

It will be scarcely necessary to state in detail the particular bearing which the preceding considerations have on the question of the mechanism of the absorbent process in the living body. It is, however, very evident that they leave us with little more than some

* In a valuable paper by our friend, Dr. Robinson, of Newcastle (Med. Gazette, 1844) many experiments and arguments are given to show that absorption goes on rather on the venous side of the capillary network, and in the small veins, than on the arterial side. He considers the motion of the blood to be an influential cause of absorption, by diminishing its pressure outwards on the vascular walls, and thus allowing the external pressure (that of the atmosphere and of the surrounding tissues) to predominate. There can hardly be a doubt that the rapidity of absorption would be influenced by the rate of movement of the blood as well as by other mechanical conditions.

general indications of the lines in which further investigation may be pursued with advantage.

Applying them to the mechanical arrangements provided in the living animal for this function, it is plain that they have a nearer reference to the capillary blood-vessels than to the lymphatics. In both we have a simple membrane of extreme thinness, through which the absorbed fluid has to pass, and in doing so it must necessarily obey those laws which form the proper subject of experimental physico-chemical inquiry. But in the blood-vessels, the fluid on the side towards which absorption tends is already in motion by a mechanical force, the heart's action, and the absorption is accompanied with a contrary current of exosmose; whereas in the lymphatics, the internal fluid appears to have no motion but what is derived from the same force on which the endosmose depends, and we have no evidence of any outgoing current. In these respects the absorbents resemble more nearly than the capillaries, the spongioles and absorbent vessels of plants.

Function of the Absorbents.—A few words may be added on the use of the absorbents in the œconomy. The *chyliferous vessels* probably have the same office for the intestinal tissues as the lymphatics in other parts; but besides this they are largely developed, and specially adapted by their mode of origin on the mucous surface, to take up a portion, at least, of the food, after it has been rendered capable of absorption by the action of the pancreatic secretion. This portion appears to be pre-eminently the fatty or oily, which, as far as experiments and observation have yet determined, is almost exclusively absorbed by the lacteals. It is chiefly in containing so much more fat that chyle differs from lymph.

The *lymphatics* cannot yet be said to have their office at all definitively ascertained, yet it is not difficult to assign them a part with some degree of probability. It appears that they form an interlacement among the capillaries in the interstices of most of the organs and tissues of the body, and contain a fluid not dissimilar in kind from the liquor sanguinis, though more dilute. They cannot be engaged in distributing new material to the organism, because their structure adapts them only for removing fluid from the tissues, and pouring it into the blood-vessels, and because the current within them is unequivocally in that one direction. Thus the fluid they contain must enter them from the interstices of the tissues, having been ultimately derived either directly from the capillaries, or indirectly from them through the tissues. It seems not improbable that the liquor sanguinis effused through the capillary

walls for the nutrition of the tissues, may have its superfluous parts removed through the lymphatics, as it would, perhaps, be more readily received into these new channels than into the same from which it had just been poured. It is a question quite undetermined, whether the effete materials of the tissues are returned to the circulation in any large measure through the lymphatics, or whether they are principally restored to it by directly entering the capillaries, in exchange for that outgoing current of renovating plasma which serves to supply the waste in nutrition. The carbonic acid at least, if indeed that product be formed among the tissues, outside the capillaries, and not in the blood, seems to enter the capillaries in a direct manner through their wall, since it is found in greater quantity in venous than in arterial blood.

The absorbent system, with its glands, may be regarded in yet another light, viz., as a great internal glandular or secreting system, the ducts of which open not on the surface of the body, but into the vascular system. It is conceived that the inner surface of the lymphatics, and especially of the lymphatic glands, serves to elaborate and separate from the blood contained in the vessels distributed on their walls a secretion which is set free into their interior, and is transmitted ultimately to the current of circulating blood through the efferent vessels of the glands, which may be thus looked upon as excretory ducts. Some physiologists attach much importance to the alleged increase in the quantity of fibrine contained in the lymph as it traverses the absorbent system, and conclude that this is due to the elaborating agency of the epithelial element of the absorbent tracts on the albumen of the lymph. We owe to Dr. Carpenter a very interesting hypothesis on the influence, in this respect, of the colourless corpuscles, which he imagines to exert this catalytic action on the albumen in which they float. This idea will be best considered in the Chapter on the Blood.*

* On the subjects of the foregoing chapter, in addition to the systematic works on Physiology before referred to, the student may consult Mr. Lane's article "Lymphatic System," in the Cyclopædia of Anatomy and Physiology; Matteucci's "Lectures on the Physical Phenomena of Living Beings," translated by Pereira; and the valuable "Reports" by Mr. Paget, in the British and Foreign Medical Review. We would also refer to a recent work by Liebig, on the motion of the juices of the animal body, ably translated by Dr. Gregory, from which we have derived much assistance.

CHAPTER XXVII.

THE BLOOD.—ITS QUALITIES.—ITS PHYSICAL ANALYSIS.—THE LIQUOR SANGUINIS. — THE BLOOD PARTICLES. — THE QUANTITY OF BLOOD IN THE BODY.—THE PHENOMENON OF COAGULATION.—THE CONSTITUENTS OF THE BLOOD.—ANATOMY OF THE BLOOD CORPUSCLES.—THEIR MODE OF ORIGIN. — THEIR FUNCTION. — THE CHEMICAL ANALYSIS OF THE BLOOD.—CHANGES PRODUCED IN THE BLOOD BY VENESECTION,—AND BY DISEASE.

The blood is a fluid, which is always circulating in numberless canals among the various tissues and organs of the body; it is the source whence those tissues and organs draw their nutriment, and from which the glands derive the materials for their several secretions. The lymph and the chyle are poured into it as tributary streams; the former conveying to it, in solution, materials yielded up by the wear and tear of the tissues, and also derived from without; the latter bringing to it new matter formed by the digestive process.

The blood is a thick fluid, apparently homogeneous, of high specific gravity (1041—1082, Simon,) and of a red colour, in all the vertebrate and most of the invertebrate classes, but exhibiting differences of colour, according to circumstances to be noticed hereafter. A saltish taste, and a peculiar heavy odour, must also be reckoned among its characters. If allowed to rest in a cup, or other vessel, it exhibits a remarkable spontaneous analysis. In the course of from ten minutes to half an hour it separates into a solid portion (the crassamentum) and a fluid portion (the serum). The latter, if carefully decanted off, will be found to be a clear straw-coloured fluid, the menstruum of that great variety of materials which is held in solution or suspension in the blood. Albumen in large quantity, salts, and various organic matters, are dissolved in it; oily matters are suspended in it; and prior to coagulation fibrine is held in solution, and coloured and other particles are diffused in infinite multitudes throughout it.

An artificial physical analysis of the blood, first suggested by Müller, shows satisfactorily the true relation of its various constituents. If the blood of an animal whose coloured particles are

of large size, as the common frog, be passed through filtering paper, its liquid portion passes through, leaving the coloured particles upon the filter: thus analyzing the blood into two parts —*the liquor sanguinis* and *the blood particles.* The former, by the spontaneous coagulation of the fibrine, quickly separates into serum and fibrine, which in this instance is colourless, but in the ordinary coagulation it is more or less coloured by the red particles, which become entangled by the coagulating fibrine. Another mode of effecting a similar analysis is that suggested by Dr. A. Buchanan of Glasgow: it consists in mixing fresh-drawn blood with six or eight times its bulk of serum, and filtering through blotting-paper: coagulation is retarded by the admixture with serum, and a great part of the diluted liquor sanguinis passes through the filter, and subsequently coagulates. By microscopical analysis of the blood we find, that, besides the red particles, it contains others which are devoid of colouring matter—namely, the *colourless corpuscles.*

The constitution of the blood is expressed by the following table:—

$$\text{The blood consists of}\begin{cases}\text{corpuscles; red and colourless.}\\ \text{liquor sanguinis, consisting of}\begin{cases}\text{fibrine.}\\ \text{serum.}\end{cases}\end{cases}$$

That the blood has the same essential characters in both the vertebrate and invertebrate classes has been shown by Mr. Wharton Jones's researches, who finds the coloured and colourless corpuscles in the blood of all animals, presenting, however, sufficiently distinctive features.

In man and the mammalia there are two kinds of blood, distinguished by difference of hue, *the scarlet, arterial blood*, obtained from the left side of the heart, and from the arteries: and the *black*, or *dark red, venous blood*, obtained from the right side of the heart, and from the systemic veins. We shall consider further on the special characters of each kind, and the cause of their differences.

The temperature of the blood ranges between 100° and 105°. Its reaction is slightly alkaline, so that a drachm of blood will saturate rather more than a drop of vinegar.

The consideration of the natural history of the human blood involves the determination of the following points:—

First, the quantity of blood in the body.

Secondly, the phenomenon of coagulation, and the circumstances which promote or retard it.

Thirdly, the physical analysis of the blood, and the characters of its constituents.

Fourthly, the chemical analysis of the blood.

I. *Of the Quantity of Blood in the Body.*—It is almost impossible to obtain sufficiently accurate data upon which to found a calculation of the total quantity of the blood which circulates in the vascular system. The various estimates which have been formed have been guesses, based on trials by bleeding animals to death, and comparing the weight of the blood drawn with that of the animal's body: also, on ascertaining, in various cases of hemorrhage, or of venesection, the quantity of blood which had been lost in a brief period, without destruction to life.

Harvey estimated the weight of the blood as one-twentieth of that of the body, and Haller at one-fifth. According to the former estimate, a man of one hundred and fifty pounds weight would have only about seven and a half pounds of blood, whilst the latter would assign him thirty pounds.

Valentin devised an ingenious method of estimating the quantity of the blood. He first ascertains the amount of solid constituents in a certain quantity of blood, withdrawn by venesection: this is replaced by a certain quantity of distilled water, and then he ascertains the amount of solid constituents in a quantity of the now diluted blood equal to that which had been first withdrawn. From the data thus obtained he calculates the whole quantity of the fluid, which admits of such a change in its specific gravity, by the substitution of a certain quantity of distilled water for the quantity of the fluid itself previously withdrawn. The problem is, to determine the quantity of fluid of specific gravity B., which, on removing from it say six ounces, and replacing those six ounces by a certain quantity of distilled water, becomes reduced to the specific gravity β. Having by this method determined the quantity of the blood in dogs, he deduces the quantity of blood in the human body by comparing the weight of men with that of dogs. And thus he assigns about thirty-two pounds for a man between thirty and forty years of age, and twenty-eight pounds for the female.*

On the whole, we have no right to infer that the quantity of blood in the human body exceeds thirty pounds: and, for practical purposes, we shall do well to form a much lower estimate of it, and to learn from thence how important it is to avoid being prodigal in the removal of a fluid, so essential to the phenomena of life,

* Valentin. Physiol.

—and to beware of subjecting patients to those excessive losses of blood, which, experience teaches us, too often inflict upon the general nutrition of the body a shock so severe, that it is more or less seriously affected by it ever after.

II. *The Phenomenon of Coagulation.*—We have already described the separation of the blood into serum and crassamentum. In this consists the phenomenon of coagulation. In a few minutes after blood has been allowed to rest in a vessel, its surface assumes the appearance of a jelly, on which, after a little more time, drops of serum appear to ooze out here and there: these drops multiply and coalesce, so as to cover the jelly-like surface with a layer of serum, which increases so much in quantity, as coagulation advances, that the clot is at last found covered and more or less completely surrounded by serum.

The *crassamentum*, or *clot*, is a solid mass, varying much in consistence: sometimes soft and tremulous, like jelly; at other times firm, and tough almost as leather. If a section of it be made, it will be found in most instances coloured throughout, but always most deeply so at its lower half or third, the heavy red particles gravitating to the lowest part; that portion which is exposed to the air having always a scarlet tint. The surface of the clot is always slightly concave; sometimes it is remarkably so, and exhibits the appearance of a hollow cup, and on these occasions the upper layers of the clot generally consist of fibrine only, which is of a whitish yellow or buff colour, with an intermixture of colourless corpuscles entangled in its meshes. Hence blood which presents these appearances is said to be "cupped and buffed." The phenomenon is due to the more complete subsidence of the blood-particles as the clot is being formed, so that its upper layers are left quite free from colouring-matter. The clot, when this state is present, is generally small, tough, and well contracted, and it floats in a large quantity of serum.

The period required for the completion of coagulation varies very much: it commences in about two minutes after the blood has been collected in a vessel, and is rarely completed for half an hour afterwards, but more frequently the clot is not perfectly formed in less than one or two hours. After it has been formed, it will continue to contract for many hours, and to press out the serum, which will thus increase in quantity while the bulk of the clot undergoes diminution.

Coagulation appears to take place more rapidly under the influence of a high temperature, 114° to 120°, according to Hewson; it

is also favoured by spreading out the blood on a flat surface; and, within certain limits, by an increase in the fluid parts of the blood.

On the other hand coagulation is retarded by the addition of alkalies, and some of their salts, as sulphate of soda, nitrate of soda, carbonate of soda, chloride of sodium, also carbonate of potass, nitrate of potass, and nitrate of lime. A strong solution of any of these salts, added to fresh drawn blood, will delay or stop its coagulation according to the strength and quantity of the solution.

Authors affirm that the blood will not coagulate in the bodies of animals killed by blows on the epigastrium, or after having been long hunted, or by electricity or lightning. It will not coagulate after asphyxia by carbonic acid, as in the following cases, recorded by Mr. Gulliver:—A man, ætat. thirty-five, and three children, were suffocated in a burning house, their bodies being untouched by the fire; in all of them the blood was fluid forty-eight hours after death in the heart and great vessels, and did not coagulate after its removal out of the body.

The coagulation of the blood appears to be retarded by its contact with living surfaces. Thackrah's experiments showed that blood confined between two ligatures in living vessels, remained fluid for a considerable time, from five to sixty minutes; F. Simon affirms that it will retain its fluidity for three hours; and experiments of the same kind by Hewson, lead to the conclusion that the coagulation is retarded under similar circumstances. Fluids withdrawn from serous cavities, as in ascites or hydrocele, often exhibit a coagulum of considerable size, which does not form till some minutes after their removal, showing that the fibrine must have been prevented from coagulating so long as it remained in the living cavity.

The addition of bile retards or prevents coagulation, probably by the mechanical obstacle which it affords to the cohesion of the particles of fibrine. According to John Hunter the addition of a solution of opium to the blood retards its coagulation.

It is needless to waste time in inquiring into the cause of coagulation. That the phenomenon belongs only to one of the constituents of the blood is proved, unequivocally, by the fact that if that material, the fibrine, be removed by whipping blood with a bunch of twigs, as it flows from a vein, coagulation will not take place in the fluid which remains. The fibrine has accumulated in a coagulated state round the twigs, and the fluid received into the vessel consists

only of serum and red particles. The coagulation of the fibrine of the blood is one of those ultimate facts in physiology which we must be content to observe and to describe, but of the cause of which we are likely to remain ignorant.

The *buffing* and *cupping* of the blood has long attracted the notice of observers, and is regarded by many practical men as an indication of a state of inflammation in some part of the body at the time of the abstraction of the blood. The immediate cause of this phenomenon is explained with the highest probability, as follows, by Dr. Babington :—

"The blood, consisting of liquor sanguinis and insoluble red particles, preserves its fluidity long enough to permit the red particles, which are of greater specific gravity, to subside through it. At length the liquor sanguinis separates by a general coagulation into two parts, and this phenomenon takes place uniformly throughout the liquor. That part of it through which the red particles had time to fall, furnishes a pure fibrine or buffed crust, while that portion into which the red particles had descended furnishes the coloured clot." The following experiment, made by the same ingenious observer, illustrates the truth of the explanation given by him. "Take two similar tall jars or phials, each capable of holding about four or five ounces, and let one of them be half-filled with olive oil; draw the blood of a healthy subject into each. That which flows through the oil will be found to have a layer of Liquor Sanguinis on its surface, which will form a buffed crust, while there will be none upon that which is received in equal quantity, and in other respects under the same circumstances, into the empty jar."*

According to the observations of Nasse, and of Mr. Wharton Jones, the red particles of blood which is disposed to become buffed and cupped, exhibit a remarkable tendency to cohere in the form of rolls, like piles of coin, and this probably facilitates their precipitation to the lowest part of the coagulating mass.

The circumstances which favour the formation of the buffy coat may be any or all of the following. 1. Slowness of coagulation; 2. Increased weight of red corpuscles; 3. Diminished specific gravity of serum, which obviously would have a corresponding effect to the preceding; 4. A great diminution in the proportionate quantity of the red corpuscles, or an increase in that of fibrine, and of colourless corpuscles. The occurrence of the cupped and buffed blood, after great hemorrhage, or in cases of anæmia, is very

* Med. Chir. Trans., and Cyclop. Anat., art. Blood.

probably in a great degree due to the disproportion between the red particles and the fibrine.

Although the phenomenon of cupping and buffing frequently occurs in that state which is called inflammatory, it is not so exclusively confined to it as to justify practitioners in regarding it, as is too often done, as a proof of the existence of inflammation, sufficient of itself to warrant or call for further depletory measures.

III. *The Physical Analysis of the Blood.*—By physical analysis we find in the blood the following parts; viz. the serum; the fibrine held in solution in the serum prior to coagulation; the red corpuscles, and the colourless corpuscles, both of which float in the Liquor Sanguinis.

The serum is a straw-coloured fluid of Sp. Gr. 1025 to 1030. When heated to 165° it becomes nearly solid, proving that it holds in solution a very large quantity of albumen, as much as seven or eight parts per cent. In twelve ounces of serum there would, therefore, be nearly one ounce of albumen equal to the white of one egg. But this is not the only ingredient which we find dissolved in the serum. It is an alkaline fluid, and its alkalinity is chiefly due to the presence of free soda, and of carbonate of soda. Besides these it contains chloride of sodium, phosphate of lime and of magnesia, and probably lactate of soda.

The serum also contains a small quantity of fatty matter in which can be detected the crystallisable as well as the oily portion. In health the proportion of this does not exceed half a part in 1000 parts, so that a pint of serum will contain about five grains of fatty matter; but in some cases it exists in so large a proportion as to render the serum milky. This occurs not only in certain forms of disease, but likewise, according to Drs. Buchanan and R. D. Thomson, very shortly after the ingestion of food of an oily or amylaceous nature.

Whatever other elements may exist in the blood, as serving to furnish materials for the various secretions, are held in suspension or solution by the water of the serum. Thus, urea is sometimes found in it, and the recent observations of Bernard, referred to at p. 261, show that it constantly contains sugar; when the liver acts imperfectly, some of the elements of bile are found in it.

It is as yet uncertain whether the existence of even minute quantities of some of these substances in the blood, such as urea and the biliary matters, is consistent with health. It is not

* Med. Gaz. vol. xxxvi., p. 972.

improbable that they may be constantly being developed by the chemical changes which are unceasingly going on in that fluid, but that they become attracted from it as quickly as they are formed in it, and do not accumulate in it in any quantity which admits of being easily detected. According to Dr. Thomson, sugar may be always easily detected in the blood, shortly after a meal containing starch.*

The Fibrine.—We have already explained the manner in which fibrine may be obtained from the blood. One thousand parts of healthy blood contain two or three of fibrine. A pint of blood will therefore yield about twenty-nine grains of fibrine, adopting the highest estimate.

Pure fibrine, or, to speak more exactly, fibrine separated from the *red* corpuscles, for it cannot be completely separated from the colourless corpuscles, has a remarkable tendency to assume the fibrous form. A drop of the colourless liquor sanguinis, which is found on the surface of blood, about to form a buffy coat, exhibits, when coagulated, an intricate interlacement of minute fibres. Here and there a colourless cell is entangled in it, appearing as a centre, whence pass numerous radiations of minute fibres. Dr. W. Addison, who believes that the fibrine is contained within the colourless corpuscles, considers the bursting of a large number of these, and the consequent liberation of their enclosed fibrine, as the first step in the process of coagulation, which explains the entanglement of them in the fibrillating fibrine. The process may be best seen, as this excellent observer recommends, by examining a drop of the colourless liquor sanguinis from blood, about to form a buffy coat, and allowed to coagulate upon a slip of glass.†

The Red Corpuscles.—It is to the multitude of coloured particles which float in the liquor sanguinis, under the name of "the red corpuscles," that the blood owes its colour. To examine these, it is only necessary to place a drop of blood in the field of the microscope, taking care to dilute it with a fluid, similar or nearly so in specific gravity to the serum: a solution of sugar or of salt in water, answers this purpose completely. So numerous and so crowded together are the corpuscles in a drop of blood, that it would be difficult to obtain a complete view of any one of them without this precaution.

In the human blood, the coloured corpuscle is a circular double concave lens; from being concave on each surface, its margin is thick and rounded, and its thickness is less in its centre than at

* *Loc. cit.* † Dr. W. Addison's second series of Exp. Researches, 1843.

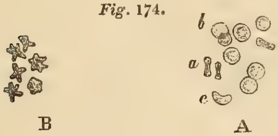
any other part (Fig. 173). Its size varies considerably: in the same drop of blood there are corpuscles of all sizes within a range of from $\frac{1}{4000}$ to $\frac{1}{2800}$ of an inch in diameter, the average being from the $\frac{1}{3500}$ to $\frac{1}{3200}$. With a good microscope, and a magnifying power of 200 diameters, the characters of the blood-corpuscles may be most clearly seen, and when the instrument is perfectly adjusted, the double concave surface may be unequivocally demonstrated. If the corpuscles are floated in water, they become biconvex: if in a fluid denser than serum, as in a strong saline or saccharine solution, they shrink, put on a shrivelled aspect, and become granulated on their surface (Fig. 174, B); this shrivelled appearance may again be got rid of by diluting the menstruum and reducing its specific gravity to the lowest point.

Fig. 173.

Red corpuscles from human blood:—*a*. Viewed on the surface. *c*. Viewed in profile. *b*. An aggregation of the corpuscles in a roll. Magnified 400 diameters.

It has been affirmed, by Mulder and others, that the blood-corpuscles of venous blood are biconvex—those of arterial being biconcave—and they attribute the difference of colour of these two kinds of blood to the different mode in which the light is reflected from the concave and the convex surfaces of their respective corpuscles. With reference to this doctrine, we have only to state that we have carefully examined two portions of the same blood after they had been agitated in oxygen and carbonic acid gas, and thus been rendered respectively scarlet and purple, but that we have failed to detect any well-marked difference in shape between the blood-corpuscles of the two specimens.

Fig. 174.



Red corpuscles of the ox, magnified 400 diameters. A. In their natural state. *a*. Profile view. *b*. Viewed on the surface. *c*. A corpuscle altered in shape. B. Corpuscles altered by a menstruum of high density.

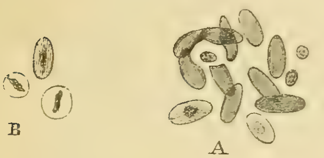
The blood-particles have a remarkable tendency to aggregate in rolls like pieces of coin (Fig. 173, *b*): this tendency, as has been already remarked, is said by some to be greatly increased in blood which forms a buffy coat in its coagulation.

The red blood-corpuscle of Mammals resembles in shape and structure that of man (Fig. 174): there is much diversity of size in the various orders; it is smallest in the ruminants, and the smallest known is that of the Napu musk-deer, which is reported by Mr. Gulliver not to exceed $\frac{1}{12000}$th of an inch in diameter. The

corpuscles of the goat are very small, $\frac{1}{6300}$—$\frac{1}{7045}$ of an inch in diameter. The largest corpuscles in Mammalia are found in the elephant; they measure, according to Gulliver, $\frac{1}{2745}$ of an inch in diameter. The Camelidæ offer a remarkable exception to the circular form of the blood-corpuscle of Mammalia. In these animals it is oval, as first pointed out by Mr. Gulliver, with a long diameter of from $\frac{1}{3100}$ to $\frac{1}{3550}$ of an inch, and a short diameter of $\frac{1}{5800}$ to $\frac{1}{6444}$; in all other respects, however, these corpuscles agree with those of other mammals.

In Birds the corpuscles are oval in shape; they have a very distinct nucleus, which is much smaller than the corpuscle itself. The long diameter of the blood-corpuscle of Birds ranges between $\frac{1}{1500}$ and $\frac{1}{2000}$ of an inch, and the short diameter from $\frac{1}{3000}$ to $\frac{1}{4000}$ of an inch. (Figs. 175, 181, 183).

Fig. 175.



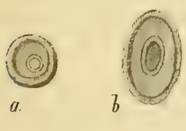
Red corpuscles of pigeon's blood magnified 400 diameters. A. Red particles unaltered, with two or three colourless particles. B. Treated with acetic acid, which developes the cell-wall and nucleus more clearly.

Fig. 176.

Blood-corpuscles of the common frog. Magnified 400 diameters. A. In serum. *a*. Fully developed corpuscle. *b*. Nucleus with pale cell-wall and clear contents. *c*. Colourless corpuscle. B. Treated with acetic acid.

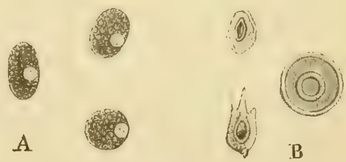
In Reptiles the red corpuscles are of an oval shape, with a distinct and large nucleus (Fig. 176). The long diameter of the corpuscle has a range of from $\frac{1}{420}$ to $\frac{1}{1440}$ of an inch, the short diameter ranging between $\frac{1}{760}$ to $\frac{1}{2600}$ of an inch. Among these are to be found the largest known blood-corpuscles, as those of the proteus and of the syren.

Fig. 177.



Red corpuscle of fishes:—*a*. Lamprey. *b*. Skate. (After Wharton Jones.)

Fig. 178.



Blood-corpuscles of the crab. A. Granule cells. B. Nucleated cells. (After Wharton Jones.)

In Fishes, the red corpuscle is oval in most of the genera, and possesses a distinct nucleus (Fig. 177, *b*). In the lowest cartilaginous fishes, as the lamprey and the myxine, however, it returns to the circular and biconcave form of the Mammalian red corpuscle (Fig. 177, *a*). This remarkable fact was first pointed out by Professor R. Wagner. Mr. Wharton Jones has shown that it contains a nucleus, which cannot be detected in the red corpuscles of Mammalia.

In the Invertebrate classes, corpuscles exist which are in close analogy with those of the Vertebrata, but differ from them in several particulars (Fig. 178). They are nucleated cells, some of which contain within them numerous granules which conceal the nucleus; some of these corpuscles, according to Mr. Wharton Jones, are, upon their first removal from the body, of an elongated oval form, and others spindle-shaped. Their size does not exceed $\frac{1}{2000}$th of an inch in their long diameter, nor $\frac{1}{3000}$th in the short. In most of the classes the particles do not exhibit any indication of colour, although they contain some of the ingredients of hematine; in a few, however, slight traces of colour are present.*

Of the Structure of the Red Corpuscle.—The structure of the red corpuscle of most of the vertebrata may be readily demonstrated in the blood of Reptilia—that of the frog, for instance. It is distinctly a nucleated cell—consisting of a delicate cell membrane, within which is a granular nucleus, which may be rendered more distinctly granular by acetic acid (Fig. 176, B). The nucleus is globular and much smaller than the cell, and the interval between the inner surface of the latter and the outer surface of the former is filled by fluid which holds the colouring matter in solution. Corpuscles of this kind floated in pure water become distended by the endosmosis of it, burst and give exit to their nuclei, while the shreds of the cell-membrane are scattered in the fluid.

It cannot be shown satisfactorily that the biconcave circular corpuscle of human blood and of that of mammalia is of the same structure as this, because it cannot be demonstrated to consist of cell and nucleus. If it be, as the blood-corpuscles of birds, reptiles, and fishes undoubtedly are, a nucleated cell, the obscurity of its nucleus is probably due to one of two causes; either it is so large as accurately to fill the cell, leaving no space between the outer surface of the one and the inner surface of the other, or it is so extremely minute as completely to elude our means of observation.

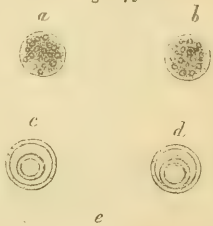
Mr. Wharton Jones supposes that the mammalian red corpuscle is a nucleus, the cell of which had existed only in the earlier stages of development. Kölliker, on the other hand, affirms that the nucleus disappears while the cell-wall is persistent. All that microscopic examination with the highest powers and the best instruments shows respecting the structure of this corpuscle is that it consists of a delicate membrane, enclosing a semifluid material, impregnated with the proper colouring matter of the blood; and that this

* Mr. Wharton Jones' papers in the Phil. Trans. for 1846, "On the blood-corpuscle considered in its different phases of development in the animal series," contain an account of a careful examination of these particles, and may be referred to with advantage by all who are engaged in the study of this most interesting subject.

structure may truly be assigned to it is amply proved by the change of form, which it undergoes by the endosmosis of pure water, which will cause it to burst and evacuate its contents, consisting of nothing more than some minute granules, none of which can be compared to a nucleus. So far as microscopic analysis would enable us to decide this question, we should be disposed to declare in favour of Mr. Jones's view; but it seems greatly opposed by two facts; first, that in the corpuscle of the lower vertebrata, the colouring matter is contained between the nucleus and the cell-wall, whereas in the mammalian corpuscle it would be contained in the nucleus; and, secondly, that this peculiarity of structure is limited to one class of vertebrate animals. It receives support, however, from observing the several steps of the development, for the corpuscle exhibits a stage in which a nucleus is visible (the stage of coloured nucleated cell), (Fig. 179, *d*), and this nucleus in the very large corpuscle of the elephant, and likewise in the very small corpuscle of the goat, exhibits a strict correspondence in size with the perfectly formed blood-corpuscle. But here, again, we notice the difficulty above referred to, that in this stage of nucleated cell, the colour is found between the cell and the nucleus. It seems to us that further research is required, in order to determine the exact homology of the mammalian red corpuscle.

The Colourless Corpuscles.—These particles are found in all kinds of blood. They are spherical bodies, destitute of colour; their structure is that of nucleated cells, the cell-membrane being extremely delicate; both the cell membrane and the nucleus and nucleolus are rendered distinct by the action of dilute acetic acid, which dissolves some granules which are contained in the cell. These granules are external to the nucleus. When they are numerous and large the nucleus is concealed by them. Corpuscles of this kind, denominated *granule cells* by Mr. W. Jones (Fig. 179, *a*, *b*), are viewed by him as constituting an earlier stage than those in which the nucleus and nucleolus are distinct, which he calls *nucleated cells* (Fig. 179, *c*, *d*). In size the colourless corpuscles slightly surpass the red corpuscles in mammalia; but not in the other vertebrata. They are essentially the same as the nucleated particles found in lymph and in chyle. In

Fig. 179.



Phases of the human blood-corpuscle (after Wharton Jones). *a* and *b*. Granule cells in the coarsely and finely granular state. *c* and *d*. Nucleated cells, *c*. without colour, *d*. with colour. *e*. Free cellæform nucleus or perfect red corpuscle.

examining the capillary circulation in the transparent parts of some animals, as the web of the frog's foot, they may be seen sparingly at the margin of the current of red corpuscles, either stationary and adherent to the wall of the blood-vessels, or slowly moving forward in the layer of liquor sanguinis which is in contact with the wall, and which is thus shown to be comparatively motionless.

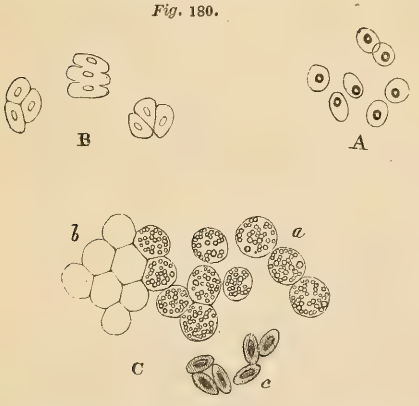
The colourless corpuscles are much fewer in number than the coloured; it is said that they exist in the proportion of one colourless to fifty coloured, but that in inflammatory states of the blood, the former are much more numerous, being as one in twelve. After great loss of blood, the proportion of the colourless corpuscles is considerably increased.

A very important inquiry is to determine—1. The histological relation of these particles to each other; and, 2. The part which they take respectively in the vital phenomena of the blood.

With regard to the first point, physiologists are divided in opinion as to whether they may be regarded as distinct and independent particles, performing each their special functions, or whether the one, namely, the colourless corpuscle, may be viewed as an early or embryo condition of the red corpuscle.

The weight of argument seems to favour the conclusion that the colourless corpuscles are to be regarded as an early stage of the coloured corpuscles, which are in the adult or perfect state. In the earliest periods of fœtal life, the blood-corpuscles, as is shown by the researches of Vogt, Kölliker, and Cramer, originate, in the same way as the elements of the tissues, from nucleated cells, which are the same in point of constitution as the colourless corpuscles; with this exception, that they contain between the nucleus and the cell, a considerable number of granules, which are largest at the earliest periods of embryonic life. At later periods similar nucleated cells

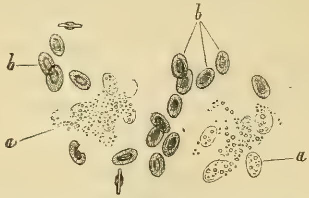
Fig. 180.



Corpuscles from the bloodvena of the cava hepatica of the embryo chick on the twentieth day of incubation. A. Red blood-corpuscles altered by water. B. Blood-corpuscles coherent and modified in shape by cohesion. C. *a*, Large spherical cells containing highly refracting granules (fatty); *b*, the same represented only in outline, to show their shape; *c*, fully formed red corpuscles. Mag. 200 diam.

are generated in the liver, as first pointed out by Weber, and in the mesenteric and lymphatic glands, and from these sources supplied to the blood. In this fluid they undergo a transformation into the completely formed blood-corpuscles, by the removal of the granules, the increased development of the nucleus, and the generation of colouring matter, excepting in the mammiferous corpuscle, whose ultimate change seems to consist in the complete absorption of the nucleus, according to Kölliker, or the removal of the wall of the cell, according to Wharton Jones.

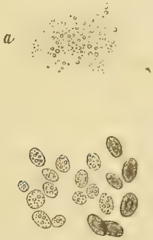
Fig. 181.



Granules, granule-cells, and red blood-corpuscles from the embryo chick at the twentieth day of incubation. *a a*, Granules, some being enveloped by a faint cell-wall, and granule-cells with coarse granules. *b b*, red blood-corpuscles. Mag. 200 diam.

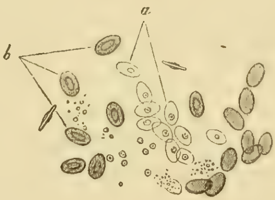
Now as there can be no doubt that in the adult the lymphatic and chyliferous systems, afford a source for the constant development of particles identical with the colourless corpuscles, and as such corpuscles are always found in considerable proportion in the blood (being more numerous under circumstances unfavourable to normal changes, as in inflammations), it seems very reasonable to infer that similar transformations of colourless into coloured particles are going on in the adult as in the embryo, and that the lymphatic and lacteal systems must be at least one, and that a fertile source, from which red corpuscles are being continually supplied to the blood.

Fig. 182.



a. Granules of which the cell-wall is not visible. *b*. Granule-cells and red corpuscles. Mag. 200 diam.

Fig. 183.



Nucleated cells, (*a*), red corpuscles, (*b*), and granules from the chick on the 20th day of incubation. Mag. 200 diam.

If, however, we reject this view of the relation of the colourless to the coloured corpuscles, then we must regard them as independent particles, each having its special function, and it devolves upon the advocates of this view to suggest the office, and to explain the mode of origin and decay of each.

Function of the Red Corpuscles.—It is clear that the red corpuscles must perform some very important office in the life of the blood, because of their great numbers, their constancy, and the serious consequences to the general nutrition and the vital actions of the body, which ensue upon any considerable diminution in the quantity of them. But we have no definite knowledge on this subject, and all that can be suggested is, as yet, of a speculative and hypothetical nature.

Liebig adopted the highly ingenious notion that the red corpuscles are carriers of oxygen, and that by their colouring matter they are peculiarly adapted for attracting that principle. The property of attracting oxygen is due to the iron, which forms six per cent. of the hematine contained in the red corpuscle. In venous blood, according to Liebig, the iron is in the state of *carbonate of the protoxide* of iron; this, as the blood passes through the capillaries of the lungs, or becomes otherwise exposed to the action of the air, is by the absorption of oxygen converted into *the hydrated peroxide* of iron, the state in which that metal exists in arterial blood. And at the same time it gives off "for every volume of oxygen necessary for the change from protoxide to peroxide, four volumes of carbonic acid." As the arterial blood passes through the capillaries of the system, the peroxide of iron yields oxygen to certain constituents of the body, which is employed in producing the change of matter, and in oxidising newly-formed substances in the blood, while in their return towards the heart, the red particles which had lost their oxygen "combine with carbonic acid, producing venous blood; and when they reach the lungs an exchange takes place between this carbonic acid and the oxygen of the atmosphere."

This doctrine of Liebig assigns the use of the colouring matter, or of the contents of the blood-corpuscle, rather than of the corpuscle itself; it is, indeed, highly reasonable to suppose that the hæmatine has an important connection with the attraction of oxygen into the system, or to speak more generally, with the changes which take place in the blood in respiration. The difference of colour, being the prominent feature of distinction between arterial and venous blood is strongly indicative of this; and also the fact now demonstrated by Mr. Wharton Jones, that the blood of the invertebrata contains a certain degree of colour, or at any rate, even where no colour can be distinguished, according to Professor Graham's analysis, "a sensible quantity of iron, perhaps, as much as red corpuscles."

Liebig, however, does not explain why the hæmatine is invariably contained in a multitude of nucleated cells. The consideration of this point seems to us to afford the clue to determine the real function of the red particles.

The true office of the red blood-corpuscles would, probably, be most correctly described as that of forming or secreting *the hæmatine*, which in the greatest part of the animal kingdom is *coloured*, but which even, though *colourless*, appears to contain iron. These particles are floating gland-cells, as Henle suggested some years ago; they are in all essential points of structure like the secreting cells of true glands, and there is no reason why, free and floating in a liquid like the liquor sanguinis, they may not exercise upon materials dissolved in that fluid, an influence analogous to that exercised by the elementary particles of the liver, or the kidney, or the pancreas upon the blood. The matter secreted by the blood-cells is the hæmatine, which term we would here use to signify not merely the colouring matter but the entire contents of the blood-corpuscle, of which iron is an important, if not an essential ingredient, and which is coloured in the vertebrata and in some of the invertebrata. It is this hæmatine which plays an important part in the attraction of oxygen, and which by its colouring matter also exercises some important influence on the whole economy, for there seems no other source from whence can be derived all that pigment which is diffused throughout various textures, such as muscle, the nervous centres, the skin and its appendages, the eye, &c., but that which is formed in such great quantity in the blood.

Office of the Colourless Corpuscles.—If these particles do not constitute an early stage of developement of the coloured corpuscles, it is clear that they must be viewed as performing some special function in the blood, independently of the latter. R. Wagner viewed them as identical with chyle and lymph corpuscles, and assuming that in the invertebrata no coloured particles existed, he regarded the blood in such animals as identical with chyle or lymph; as, in fact, the latter fluid not yet elaborated into blood. In the blood of vertebrata, therefore, he would view these particles as chyle or lymph globules not yet transformed into blood particles.

But Dr. Carpenter has put forward a more elaborate hypothesis respecting the office of the white corpuscles. This able physiologist regards these particles as the agents in the developement of fibrine in the blood, or in the conversion of albumen or other materials of

that fluid into that "plastic" compound. This substance certainly first appears in the chyle and lymph, where these particles are found in great numbers floating in an albuminous fluid. Nor does it appear in the chyle until after that fluid has passed through the mesenteric glands, which furnish these particles in large numbers.

Dr. Carpenter regards the appearance of these colourless corpuscles or cells in the blood as a phenomenon in close analogy with the development of cells in the albumen of the seed in the vegetable kingdom, and in the yolk of the eggs of oviparous animals, and he supposes that the office of these cells is to convert crude alimentary materials into proximate principles, which again, through the agency of cells, may be converted into, or may afford the materials for the peculiar compounds which form the characteristic ingredients of the secretions, or may pass into organised tissue.*

Of the Development and Decay of the Blood-Corpuscles. — It seems to us that the view which Mr. Wharton Jones takes respecting the development of the blood-corpuscles, already described at pp. 300, 301, affords the most simple and correct explanation of the origin and development of these particles. According to it, the lacteal and lymphatic systems may be regarded as the source whence fresh supplies of blood-corpuscles are being continually furnished to the blood at all periods of life. In the early embryo, as well as in the adult, the process of the formation of the blood-corpuscle would be the same, that is, the development of a nucleated cell, which undergoes transformation into the coloured particle, the steps of the process being successively *granule cell*, *nucleated cell*, and *coloured particle* (Fig. 179). This view would lead us to regard the system of lymphatic and mesenteric glands as the seat of an unceasing generation of new particles which undergo their later stages of transformation in the blood. And it is well worthy the attention of Pathologists, as affording an explanation of the great influence which (as we learn from experience) this extensive system of glandular bodies exercises upon general nutrition.

Prior to the formation of this glandular system and the development of the lymph and chyle-corpuscles, the blood-particles are derived as nucleated cells from the cells of the germinal membrane, but they undergo essentially the same changes as in the more

* Dr. Carpenter's remarks on this subject deserve the attentive perusal and consideration of physiologists. *Vid.* Principles of Human Physiology, § 153—159. *Third edition.*

advanced periods of life. In mammalian embryos they are described "as of large size, spherical or oval, pellucid and colourless, nucleated and full of minute granules." Mr. Paget, whose description we follow, confirms the observation made by Kölliker, Fahrner, and others, of the occasional occurrence of "a process of multiplication by bi-partition of the nucleus, each of which, either by appropriating half the cell, or by developing a cell around itself, becomes the central nucleus of a new cell differing from the parent cell from which it escapes, in little except in being smaller and more generally circular." *

Of the manner in which the blood-corpuscles decay we really know nothing—no more than of the mode of decay of the elements of the tissues. The notion held, for a time, by some physiologists, that the existing particles gave birth to new ones by a gemmiparous or fissiparous generation, has no foundation in careful observation. And it is most probable that, as Mr. Paget remarks, "new corpuscles never appear to be produced from the germs of old ones: when a corpuscle is past its perfection, it degenerates and probably liquefies." "The changes of such degeneration," adds this excellent observer, "have not been clearly seen in mammalian corpuscles; but they are probably nearly similar to what occur in those of fish and reptiles: in which the old and degenerate corpuscles appear perfectly white and pellucid (not shaded or granular, like the lymph-corpuscles), smaller than they were, and in some instances, cracked, or as if eroded. The nuclei appear to degenerate with the cells, but, because of their darker and harder outlines, remain longer distinct, and often look like free nuclei, unless the dim cell-wall round them be carefully searched for. But in this process, no germ for a new corpuscle issues from the transient cell. Every new corpuscle forms itself in and from the materials of the lymph and chyle, and is perfected in the blood, and the blood is maintained by constant repetitions of this process." †

Kölliker has lately put forward the remarkable opinion that the spleen is the seat of a process of destruction or dissolution of the blood-corpuscles. We shall examine this view farther on, when we come to describe the structure of the spleen,‡

IV. *The Chemical Analysis of the Blood.*—The blood is a fluid of the greatest complexity, as must be expected, if we regard it as containing the material for the nutrition of all the tissues, as

* Kirkes' Hand-Book of Physiology, p. 65, fig. 3.

† Loc. cit. p. 70. ‡ Art. *Spleen*, Cyclop. Anat. and Phys.

well as for all the secretions. Thus, in addition to the water which forms four-fifths of it, and without which no transfer of materials could take place from it to other parts, it contains albumen for the albuminous tissues; fibrine for the fibrinous; salts, which are found in the various secretions; colouring matter, which, more or less modified, is found in the nervous matter, the skin, the eye, the bile, the urine, the cerumen; and fatty matters identical with those which are found in fat.

The researches of the last few years, in which Lecanu, Andral and Gavarret, Rees, Becquerel and Rodier, Christison, Miller, and others have taken a conspicuous part, have determined, with a very near agreement, the relative proportions in which the various staminal principles exist in healthy blood.

The following method may be adopted for this kind of quantitative analysis.* Let the blood flow at four different periods and in equal quantities into two vessels, the first and third into the first vessel; the second and fourth into the second; the weight of each should be taken.

From one portion the fibrine may be separated by whipping, or by shaking up the blood in a bottle containing small pieces of lead, the residue will consist of the serum and red particles. The weight of this, deducted from that of the whole portion of blood, will give the weight of the fibrine.

The second portion may be set aside to coagulate spontaneously; when this process is completed, the crassamentum must be taken out, and after the serum has completely drained away from it, it should be weighed. The weight of the fibrine, as obtained by the first experiment, being deducted from that of the entire clot, will give that of the coloured corpuscles. The amount of albumen may be obtained by precipitating it from the serum, and weighing it after filtration.

The general results of this method of analysis may be thus stated roughly. In one hundred parts of blood, about seventy-eight parts are fluid, and twenty-two parts solid material, and of the last, the albumen constitutes rather less than seven parts, the fibrine one-fourth of a part, and the red particles rather more than fourteen parts.

The following table gives a summary of the analysis of the blood of healthy individuals of both sexes by Becquerel and Rodier, who are among the most recent analysts.

* For a more elaborate and exact method of analysis see Mr. J. E. Bowman's "Hand-Book of Medical Chemistry," p. 133.

Composition of one thousand parts of blood *in men*, derived from eleven analyses.

	Mean.	Maximum.	Minimum.
Water . .	779	760	800
Red particles . .	141·1	152	131
Albumen . .	69·4	73	62
Fibrine . . .	2·2	3·5	1·5
Extractive matters and free salts	6·8	8	5
Fatty matters . .	1·6	3·255	1

Composition of one thousand parts of blood *in women*, derived from eight analyses.

	Mean.	Maximum.	Minimum.
Water . .	791·1	773	813
Red particles . .	127·2	137·5	113
Albumen . .	70·5	75·5	65
Fibrine . . .	2·2	2·5	1·8
Extractive matters and free salts	7·4	8·5	6·2
Fatty matters . .	1·62	2·86	1

Composition of the Red Particles, and of the Hæmatine.—The large proportion which the coloured particles form of the solids of the blood, entitles them to the most attentive consideration of Physiologists: they are more than fifty times the quantity of the fibrine, and nearly double as much as the albumen.

The red corpuscles consist, according to most chemists, of two elementary substances, globuline and hæmatine, the former is nearly allied to, if not identical with albumen, and forms the solid part of the blood-corpuscle, its cell-wall, and nucleus, when it exists; the latter is the colouring material, or blood-pigment.

The following process is recommended by Figuier for the separation of the hæmatine from the globuline.

Defibrinated blood should be mixed with at least four times its bulk of a saturated solution of sulphate of soda; the mixture must then be thrown on a filter: the fluid and some corpuscles pass through, leaving the mass of coloured particles on the filter. This must next be boiled in alcohol, slightly acidulated with sulphuric acid: the hæmatine will be thus dissolved, the colourless globuline, in combination with some of the sulphuric acid, remaining undissolved.

The next step in this process is to add to the hot solution of hæmatine enough carbonate of ammonia to remove the sulphuric acid; the fluid must then be filtered, to remove the sulphate of ammonia thus formed, and the liquor must be exposed for evaporation; when, by this means, it is reduced one-twelfth of its

bulk, it will be found to deposit hæmatine as a dark or black powder.

This hæmatine is insoluble in water, alcohol, or ether, unless mixed with some alkali, which renders it readily soluble: when burned it yields a considerable quantity of iron.

Mulder's ultimate analysis gives the following as its composition :—

Carbon	65·84
Hydrogen	5·37
Nitrogen	10·40
Oxygen	11·75
Iron	6·65

Much difference of opinion exists among chemists as to the state in which iron exists in the blood. We have already referred to the opinion of Liebig, who affirms that, in venous blood, it is in the state of protoxide, while, in arterial blood, it is in that of peroxide; and that the change of colour, from the dark red of the former, to the bright scarlet of the latter, is due to the conversion of the protoxide of iron into peroxide by the absorption of fresh oxygen at the lungs. Mulder supposes that it exists in the metallic state as a simple ingredient, as essential to the colour as its oxygen, its hydrogen, its carbon, or its nitrogen. Scherer's experience, however, would go to show that iron is not essential to the colour of the blood. He treated the red particles with sulphuric acid, so as to remove their iron, and found that their colour still remained. Hence he infers that iron is not essential to the *colour*.

The value of the administration of iron in the treatment of cases of anæmia after loss of blood, is well-known and highly-appreciated by practitioners; it remains to be determined in what way it contributes so powerfully, as it unquestionably does, to the restoration of the blood to its normal state. The fact that it does exercise a powerful influence evidently indicates its importance as an ingredient in the hæmatine. And it may be remarked that iron, even if not essential to its *colour*, may, nevertheless, be an essential ingredient of a normal hæmatine.

Difference of Arterial and Venous Blood.—The prominent difference between blood drawn from the arteries and that from the veins, is to be found in the bright scarlet colour of the former, and the dark red, almost black, of the latter. To which may be added some difference of temperature, that of arterial being one or two degrees higher than venous; perhaps also some difference as to den-

sity, but upon this point observers are very far from being agreed; and also as to the proportions of solid constituents, but on this subject likewise the reports of analysts are contradictory and highly unsatisfactory.

The blood of the vena porta is said by F. Simon to coagulate more slowly and less perfectly than ordinary venous blood; it contains less fibrine and much more fat.

Influence of Venesection and of Disease upon the Blood.—The influence of venesection, and of some morbid states upon the relative quantities of these constituents of the blood, deserves to be well impressed upon practitioners.

Venesection, or the loss of blood by any means, reduces the amount of the red particles chiefly, and the more so in proportion to its frequency; the serum is diminished in density, and the quantity of the albumen and the fat is slightly reduced; that of fibrine is not affected, nor are the extractives and salts.

The following cases from Dr. Christison illustrate the influence of venesection upon the blood.

The first is that of a middle-aged woman, who had been previously repeatedly bled for palpitations of the heart. The analysis of her blood gave the following result:—

Fibrine	2
Solids of serum	76
Red particles	57
Water	863

In the second case there had been frequent bleedings after rheumatism:—

Fibrine	4
Solids of serum	93
Red particles	57
Water	844

This latter case shows how impotent is venesection, even when carried to a great extent, over the reduction of fibrine, the material that forms those new deposits of organizable matter or plastic lymph, which in inflammations of internal organs, such as the lungs and heart, so much interfere with their normal action.

The following experiment, also, illustrates the effect of venesection upon the blood, first, when the animal was well fed at the time when the bleedings were being practised; and, secondly, when it was starved between the operations.

A large dog was fed upon two pounds of meat, and a quart of milk a day, and six ounces of blood were drawn on each of four

successive days from his jugular vein. The blood was analyzed by our friend, Mr. Lionel Beale, Jun., who obtained the results shown in the following table:—

No. of Bleedings.	First.	Second.	Third.	Fourth.
Water . .	783·79	810·89	815·18	813·04
Fibrine . .	2·42	4·72	4·34	3·99
Solids of serum .	70·94	70·85	69·92	76·01
Blood-corpuscles	142·85	113·54	110·58	106·95
	1000·00	1000·00	1000·02	1000·00
Density of serum	1025·8	1024·8	1023·5	1023·6

Here, notwithstanding the liberal allowance of food, the red particles suffered a considerable diminution.

The dog was now allowed to recover, and was well fed for three weeks, and at the end of that time his blood was analyzed; he was, then, starved for four days, being allowed nothing but water, and on each of these four days was bled. The following table gives the result of these analyses:—

No. of Bleedings.	First.	Second.	Third.	Fourth.	Fifth.
Water . .	802·71	804·40	805·44	838·30	849·84
Fibrine . .	2·28	1·91	3·95	5·26	5·13
Solids of serum .	74·13	72·61	71·46	68·46	71·62
Blood corpuscles	120·88	121·08	119·15	87·98	74·21
	Dog fed.	Dog starved.			

In the latter experiments we notice a diminution of the red particles to an extent even more marked than in the former; and it may also be observed that even after a lapse of three weeks, with good feeding, the red particles had not recovered their original amount.

With reference to the estimate of the quantity of fibrine it is right to observe, that, both in these and all other analyses, it is liable to an important source of fallacy, which arises from the impossibility of forming a separate estimate of the quantity of the colourless corpuscles which adhere to the fibrine, and must necessarily increase its apparent quantity.

The modifications which disease produces in the relative quantities of the blood-constituents, are chiefly referable to an increase (real or apparent) in the quantity of fibrine, or a diminution of that element, or of the blood-corpuscles; or, lastly, to such an alteration in the quality of the fibrine (its quantity being unaltered) that its coagulating power is materially interfered with.

In diseases of an inflammatory type, in which there is active fever of a sthenic character, with proneness to the effusion of plastic lymph, or to the formation of thick laudable pus, fibrine is said to be increased in quantity to as much as five or six parts in one thousand of blood ; it is also said that there is an increase in the colourless corpuscles, and at first a slight increase in the coloured corpuscles, though these latter afterwards undergo a diminution, which is the more marked in proportion to the extent of depletory measures employed. In no diseases are these changes in the blood more conspicuous than in rheumatic fever, pneumonia, and pleurisy. The cupping and buffing of the blood is very marked, and the most exquisite examples of that interesting phenomenon may be obtained from patients labouring under these maladies. Sufficient allowance, however, does not seem to have been made by observers generally for the extent to which the apparent increase of fibrine may be explained by the increase of the colourless corpuscles.*

Diminution of the quantity of fibrine, accompanied with a decrease in the red particles, occurs chiefly in fevers arising from the presence of a poison in the system. None show these changes more than those fevers which are caused by the paludal poison —namely, intermittent fevers. In rheumatic fever and in acute general gout there is a remarkable tendency to the diminution of the colouring matter of the blood, even when these diseases have been treated in the mildest manner. It would seem as if the materies morbi acted as a blight upon the red corpuscles, and prevented their developement in the normal proportions.

In some cases—especially those connected with enlarged liver

* Zimmerman, and more recently Mr. John Simon, in his valuable lectures on Pathology (Lancet, 1850, and since republished in 8vo) have advocated the doctrine, novel indeed, but most worthy of attention, that the fibrine of the blood must be regarded not as an ingredient prepared for the nourishment of certain tissues and ready to be appropriated by them, but as "among those elements which have arisen in the blood from its own decay, or have reverted to it from the waste of the tissues." Mr. Simon has been led to adopt this opinion chiefly from observing the unaltered or even increased quantity of the fibrine under bleeding, starvation, anæmia and other states of exhaustion and increased waste, and also from the fact that in these respects the fibrine is in direct contrast with the red particles which are rapidly reduced by these means. This view is also favoured by the fact noticed by Andral and Gavarret, that an improvement in the breed of an animal tended always (cæteris paribus) to increase the proportion of the red particles, *but to diminish that of the fibrine.* The small quantity of fibrine in fœtal blood, the absence of fibrine from the egg, the chyme, and the smaller quantity of it in the blood of carnivora (which feed on it) than in that of the herbivora, are additional facts adduced by Mr. Simon in support of this view.

and spleen—the diminution in the coloured particles is accompanied by a remarkable increase in the number of the colourless particles. Some cases of this condition of blood have lately been collected by Professor J. H. Bennett, who proposes for the name *Leucocythemia* (λευκος, white; κυτος, a cell; *αἱμα*, blood).*

The fatty matters of the blood are sometimes increased in quantity apparently from non-elimination. Under these circumstances the serum becomes quite milky, an appearance which is quite characteristic of this state of blood, and may be removed by ether. We have already alluded (p. 296) to the milkiness which follows the ingestion of fatty food, but which cannot be regarded as abnormal.

There is a condition of blood to which F. Simon has given the name *spanæmia* (σπανος, poor), and which is popularly called *poor blood.* This is characterized by changes in the *quality* rather than in the quantity of the blood-constituents, and especially, perhaps, in the quality of the fibrine. When the blood is in this state, hæmorrhages are of frequent occurrence, owing probably to the imperfect manner in which the coats of the blood-vessels are nourished. Purpura and scurvy are well known diseases, of which the prominent feature consists in this poorness of blood. In the former malady we have found the blood corpuscles shrivelled, and even disintegrated;† but it is difficult to determine whether this was due to a defect in their mode of generation and development, or to a diminished specific gravity of the serum favourable to its endosmose by them.‡

* Monthly Journal of Med. Science, Edinb. Jan. 1851.

† See a case.

‡ On the subject of the blood, reference is made to the works on Physiology already quoted; Hewson's works, by Gulliver (Sydm. Soc.); J. Hunter on the Blood, &c.; Mr. Gulliver's numerous and valuable observations in the appendix to the English edition of Gerber's Anatomy, and in his notes to Hewson's works; Simon's Animal Chemistry, by Day (Sydm. Soc.); Wharton Jones, On the Blood-corpuscle considered in its different Phases of Developement in the Animal Series, Phil. Trans. 1846; Kölliker über die Blut-Körperchen eines menschlichen Embryo und die Entwickelung der Blut-Körperchen bei Saugethieren; Nasse, über das Blut; Sharpey and Quain's Anatomy; Dr. Miller's article on Organic Analysis in the Cyclop. of Anat.; Andral, Essai d'Hématologie Pathologique; Becquerel and Rodier, Recherches sur la Composition du Sang, &c., 1844; Dr. Owen Rees on the Blood and Urine; Mr. J. E. Bowman's Practical Hand-Book of Medical Chemistry; Mr. John Simon's Lectures on General Pathology, 1850.

CHAPTER XXVIII.

THE CIRCULATION OF THE BLOOD.—THE SANGUIFEROUS SYSTEM.—ARTERIES.—VEINS.—CAPILLARIES.—THE HEART, IN THE LOWER ANIMALS, IN MAN.—PHENOMENA OF ITS ACTION.—COURSE OF THE CIRCULATION IN MAN.—FORCES BY WHICH THE CIRCULATION IS CARRIED ON IN THE ARTERIES, CAPILLARIES, AND VEINS.

It is difficult to comprehend how it escaped detection for so long a time that the complex fluid, the properties of which were considered in the last chapter, is perpetually in motion. Physiologists were not insensible of the importance of the blood to the general nutrition of the body; but of its relation to the elements of the various tissues, they seem to have formed no adequate idea.

The discovery of the circulation of the blood by our immortal Harvey, and first taught by him in 1619, was, perhaps, the most perfect physiological induction from well ascertained anatomical facts ever made. A careful study of the anatomy of the veins and of their valves, and also of the heart and its valves, and the comparison of the possible relation which these mechanical contrivances in the one, might bear to those in the other, led to the inevitable inference that the fluid contained in these vessels and in the heart, not only moved, but also moved in a certain and uniform direction.

The agents of the circulation of the blood, are the heart and the blood-vessels: the latter being a series of tubes of various sizes and structure, and of various vital endowments; the former, a sort of living forcing pump in free communication with this system of tubes, which, by its unceasing action, keeps the blood in continual motion.

We shall first examine the structure and vital endowments of each of these agents of the circulation, and then inquire into the part which each plays in maintaining the circulation of the blood.

Of the Blood-vessels.—The blood-vessels are of three kinds, *Arteries*, *Veins*, and *Capillaries*.

The Arteries are the vessels which convey the blood from the heart. The etymology of the term (αηρ, τηρεω), shows that it was adopted at a period when nothing was known as to the real nature of the contents of these tubes during life. The fact that so large a proportion of the arterial system is empty after death, led

to the opinion which prevailed to the time of Herophilus that it contained vital spirits or air (*spiritus* or *πνευμα*) during life, and the arteries were called *πνευματικα αγγεια*.*

Arteries are cylindrical tubes, whose walls are formed mainly by a highly elastic material, whereby the cylindrical form is preserved and the collapse of the tube is prevented. For the same reason when an artery is cut across, its mouth is patulous, and remains so.

The walls of arteries consist of three different textures:—first, the external tunic, composed of areolar tissue, and commonly called the cellular coat:—secondly, the middle coat, or fibrous tunic; and thirdly, the epithelial tunic.

The external tunic is that through the medium of which the artery is connected with neighbouring structures, and it also forms a nidus for the support of the nutrient blood-vessels of the arterial wall. These minute vessels, named *vasa vasorum*, are derived from neighbouring arteries; they ramify freely in the external tunic, and send minute branches to a certain depth in the wall of the artery. In a well-injected subject, they may be seen filled with injection on all the larger arteries, and when great vascular congestion has accompanied or preceded death, these vessels participate in the general plethora, and may be seen distended with blood on the aorta and its larger branches.

In some of the large arteries, a few pellets of fat may be found in the outer layers of the external tunic, which consist of very loose areolar tissue: the inner layers of this tunic are, however, very condensed, and adapt themselves closely to the middle coat of the artery to which they adhere intimately, probably by reason of the continuity of some of their fibres with those of the middle tunic. The same elements are found in the external coat of arteries, as in areolar tissue elsewhere, namely, the white and yellow fibrous tissue, but the former predominates in quantity so much that in some situations it seems to be the sole constituent of the tunic.

The extensibility, toughness, and power of resistance which this tunic enjoys, by reason of the large quantity of white fibrous tissue which it contains, adapt it admirably as the external investment of the arterial tube. It serves to give mechanical support to the other tunics, and being the medium in which the nutrient blood-vessels are distributed, it contributes to a certain extent to their nutrition. Hence there is no other tunic, the loss of which, an

* This idea respecting the office of the arteries is thus expressed by Cicero. "Spiritus ex pulmone in cor recipitur et per arterias distribuitur, sanguis per venas." De Nat. Deor., L. ii.

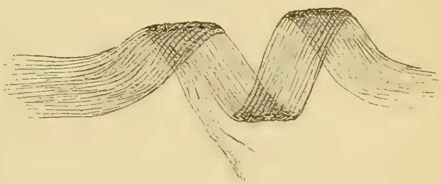
artery suffers from so much; in diseased or injured states of the other coats, it preserves the integrity of the tube, and prevents any serious interruptions to the circulation; the wall of many aneurisms consists in great part of this tunic: and on the application of a ligature, while the inner and middle coats give way under the pressure, this tunic resists and preserves its continuity for a time.

Of the Middle, or Fibrous Coat.— This tunic constitutes the principal portion of the arterial wall. It is in greatest part composed of yellow elastic fibrous tissue; but it likewise contains some white fibrous tissue, and also some of the unstriped muscular fibre.

When a large artery, as the human aorta, or the aorta of a horse or ox, is cut either longitudinally or transversely, two very distinct portions may be observed on examining the surface of the section with the naked eye. These are, an internal portion, quite yellow in colour, and constituting not more than a tenth or a twelfth of the thickness of the whole tunic; and an external portion of a grayish-yellow colour.

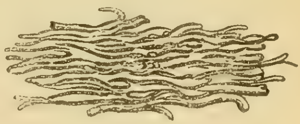
The internal portion, which we shall call *the longitudinal fibrous tunic*, is composed of longitudinal fibres of yellow fibrous tissue, disposed in two planes, forming an internal and an external layer. The internal layer is in intimate contact with the epithelium, and consists of fine pale somewhat flat not branching fibres, imbedded in a hyaline membrane which peels off readily in the length of the vessel, and when separated from connexion with the adjacent layer assumes a coiled form, as shown in fig. 184. These fibres are not altered in any degree by the action of acetic acid. The external layer is composed of fibres of elastic tissue, which also take a longitudinal direction, but are much coarser, and branch freely, forming a very intricate interlacement (fig. 185).

Fig. 184.



Finely fibrous layer of the longitudinal fibrous tunic of the aorta of the horse. Magnified 200 diameters.

Fig. 185.

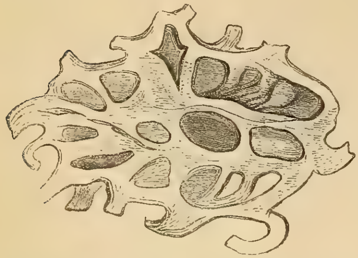


Coarsely fibrous layer of the longitudinal fibrous tunic of the aorta of the horse. Magnified 200 diameters.

The external grayish-yellow portion of the fibrous coat of arteries forms nine-tenths or eleven-twelfths of the thickness of the wall of the artery, and may be distinguished from the internal portion by the name of the *circular fibrous tunic*. It consists entirely of transverse fibres, which surround the artery at right angles to its long axis. These fibres

separate readily when pulled in the transverse direction. They form a series of concentric layers, in number proportioned to the thickness of the artery, composed of coarse yellow fibres which branch and interlace freely.

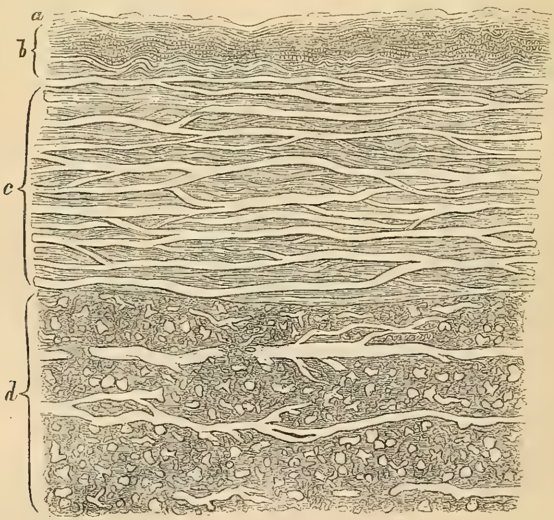
Fig. 186.



A portion of the circular fibrous tunic of the aorta of the horse, to show the reticulation formed by the interlacement of its fibres. Magnified 200 diameters.

Upon fine transverse sections of the middle coat of one of the large arteries of man, or of the ox, we may observe the peculiar arrangement of these branching fibres which gives rise to the tendency of this coat to split into lamellæ. Certain large fibres or rods of yellow elastic tissue are disposed in successive concentric circles which pass transversely, and sometimes obliquely round the artery. (Figs. 187, 189, 190). These branch in a penniform manner (hence we propose to call them *the penniform fibres*), and interlace with those on the same plane as

Fig. 187.



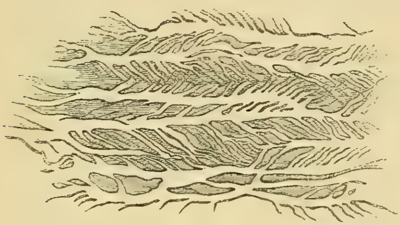
Section of the aorta of the ox, showing the arrangement of the two layers of the longitudinal fibrous tunic and of the circular fibrous tunic. Magnified 250 diameters. *a.* The epithelial tunic. *b.* The internal layer of the longitudinal fibrous tunic. *c.* The external coarse layer of the same. *d.* A small portion of the circular fibrous tunic: most of the fibres are cut across, but a few which take an oblique course are seen in their whole length, and their penniform branching is slightly indicated.

well as with those on an inner and outer plane. The branches again subdivide, and form by their frequent anastomoses that intricate

interlacement which is represented in fig. 187. This disposition of the fibres may be particularly well seen on thin sections made from the dried aorta of the ox, and afterwards moistened with acetic acid. It is also sufficiently obvious in the aorta of the human subject, but the fibres are all very much smaller, nearly one-half the size of those of the ox, and the penniform subdivision is not so distinct.

Muscular Fibres.—Interposed between the layers of penniform fibres we find some of the wavy white

Fig. 189.



A portion of the circular fibrous coat, showing the penniform branching of the large rods of elastic fibrous tissue, each large rod giving origin to multitudes of small interlacing fibres. Magnified 200 diameters.

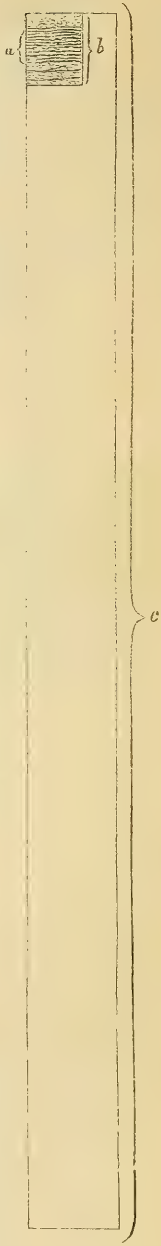
fibrous tissue also arranged in a circular form, and intermingled with this are some transverse fibres of unstriped muscle, with oval nuclei, whose long axes are at right angles to the arterial canal (fig. 191).

Fig. 190.

A single bar or penniform fibre from the circular fibrous tunic of the aorta of the ox, the small fibres having been broken off. Mag. 400 diam.

These do not seem to form any single uniform layer, but are disposed probably on different planes (somewhat like the fibres of the dartos in the areolar tissue of the scrotum) among the fibres of the circular fibrous coat, and follow the same direction. They are best

Fig. 188.

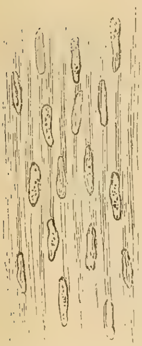


A section of the whole thickness of the artery, to show the relative extent of the portions of its walls shown in the preceding fig. Magnified 40 diameters.
a, The coarsely fibrous portion of the longitudinal fibrous tunic; *b*, the longitudinal fibrous tunic and a portion of the circular fibrous tunic; *c*, the entire thickness of the artery.

developed in arteries of the middle and smaller size, and may be most easily separated from the fibrous tissue in arteries which have undergone slight decomposition. They are then seen to consist of long fusiform fibres of much delicacy, with a minute nucleus in most of them. In the mass they have the appearance represented in fig. 191.

The external layers of the circular fibrous coat become gradually more and more like the ordinary yellow elastic tissue, the penniform and the muscular fibres cease, and the true yellow elastic branching fibre becomes continuous with that which is found in sparing quantity in the external coat.

Fig. 191.



Unstriped muscular fibres from the aorta of the horse. Magnified 300 diameters.

Epithelial Layer.—The interior of the arteries is covered by a single layer of delicate oval epithelial particles, which separate very soon after death, and must, therefore, be sought for in quite recent subjects. They may be best seen by scraping the inner surface of the artery. The long axis of each of these particles is parallel to that of the vessel. They are pointed, or, as it were, drawn out at their extremities; and, according to Henle, they are sometimes elongated into fusiform fibres. They are remarkable for the large size and the distinctness of their nuclei which are often visible when the cell wall cannot be detected. The particles seem to rest immediately upon the innermost layer of the longitudinal fibrous tunic, which bears the relation of a basement membrane to them; in this, when detached, minute apertures appear constituting the fenestrated membrane of Henle. It is possible, as suggested by Henle, that this membrane arises from the transformation of the epithelium, which is ever drawing the materials of its formation and nutrition from the blood contained in the artery. Thus it is not improbable that the innermost layers of the arterial wall, at least, are nourished from the blood flowing through the artery, and not from the blood of the *vasa vasorum*, which do not seem to penetrate to them. And this view is supported by observing that these innermost layers of the artery, *i.e.* the longitudinal fibrous tunic, are the seat of the atheromatous deposits which are so common in peculiar diatheses, or at an advanced period of life; these deposits being doubtless derived from the blood which traverses the artery.

From the preceding description it would appear that the fol-

lowing tunics may be enumerated as constituting the wall of an artery proceeding from without inwards.

Fig. 192.

Epithelial particles from the aorta of an ox. Magnified 400 diameters.

Fig. 193.

Particles of epithelium and nuclei from the aorta of a horse; some of the former exhibit the elongated character. Mag. 200 diam.

First, the external coat consisting of areolar tissue.

Second, the circular fibrous coat, consisting of a series of lamellæ, composed of yellow elastic fibrous tissue, the most external of which are intermingled with white fibrous tissue and with circular muscular fibres.

Third, the longitudinal fibrous layer, which consists of two layers, a finely fibrous, and a coarsely fibrous.

And lastly, a layer of epithelium.

The internal layer of longitudinal fibres—which is the same as that described by Henle under the name of *fenestrated* membrane—constitutes, along with the epithelium, the internal tunic so long recognised by anatomists.

The elastic reaction of arteries is evidently resident in the middle fibrous coat, and in the same tunic the contractile power of the artery resides. The existence of these two forces in the arterial wall, the one of simple elastic reaction, the other of a slow muscular contraction, is shown by the well-known experiments of John Hunter. A piece taken from each of the large arteries of a horse bled to death was laid open and extended on a flat surface without stretching; it was then measured, and afterwards subjected to strong tension, it was then measured again; on the removal of the stretching force it failed to recover itself to its first dimensions by a notable difference. When an animal has been bled to death, the

arteries are in their greatest state of contraction, the quantity of blood circulating in them being reduced to a minimum. This state of contraction Hunter assumed to be the result of muscular force, and with good reason, as, after stretching, the artery did not contract to its previous dimensions. The stretching destroyed the muscular force, leaving whatever contraction would take place, on the removal of the stretching, to be effected by the elastic force. Thus a piece of the aorta of a horse, when slit up and opened on a plane surface, measured five inches and a half; on being stretched it lengthened to ten inches and a half; the stretching power being removed it contracted again to six inches, "which," says Hunter, "we must suppose to be the middle state of the vessel."* These powers inherent in the arterial wall, of yielding under a distending force, and reacting upon its contents with a force equal to that of the primitive disturbing one, and also that of muscular contraction, exercise an important influence in promoting or directing the circulation of the blood through the arterial system.

The elastic element of the arterial tunic is always developed in the direct ratio of the size of the artery; and the muscular element, although perhaps not bearing an inverse proportion to the size of the artery, yet becomes more prominent and distinct as the elastic tissue diminishes in coarseness and in strength. Thus it is in the smaller arteries that we notice the most perfect arrangement of muscular fibres, and in these the fibrous tissue is reduced to its internal longitudinal fibrous layer, the external circular fibres having disappeared.

Blood-vessels and nerves are freely distributed to the arterial tunics. To the former, allusion has already been made in describing their external tunic. We have no evidence that these blood-vessels penetrate further than to a slight depth into the fibrous tunic. It is probable, therefore, that they are destined to nourish the external tunic, and a portion (chiefly the muscular element) of the fibrous tunic, leaving the remainder of the arterial wall to imbibe its nutrition directly from the blood itself. The general arrangement of the nerves on the outer coat of arteries has been already described (vol. i. p. 223, and vol. ii. Chap. xx.) The plexuses formed are chiefly conducted by the arteries to parts beyond: but they also furnish filaments penetrating to the muscular fibres, and bringing these into relation with the nervous system.

The arterial system may be described as taking its starting point

* Hunter on the Blood, Inflammation, &c., 4to. ed. p. 124, et seq.

from the heart, by the attachment to that organ of each of the two great vessels (the aorta and the pulmonary artery) which form the main trunks of their respective systems. The middle coat of each of these vessels is inserted into or adherent to the concavity of three festoons composed of rounded cords of white fibrous tissue. To the central portion of the convexity of each of these the muscular fibre of the heart adheres closely in the case of the pulmonary artery; but in that of the aorta, one festoon and the half of another gives attachment to muscular fibre, whilst the other half of this festoon, and a third are attached to a part of the fibrous zone, which forms the base of the inner lip of the mitral valve. Along the line of these festoons the lining membrane of the heart becoming continuous with that of the arteries forms three semilunar curtains which are strengthened by processes of fibrous tissue continuous with the festoons. These folds constitute the *valves* of these vessels, the only ones of the arterial system. We shall recur to these by and bye.

Arteries convey the blood to the various parts of the body by the subdivision of their trunks and the giving off of branch-vessels at various points. The branches for the most part come off at an acute angle with the continued trunk, so that the new stream of blood does not experience any great diversion from the direction of its parent stream. In a few instances, however, this arrangement is not observed, as in some of the intercostal and lumbar arteries, which form nearly a right angle with the aorta from which they originate.

Anastomoses of Arteries.—The manner in which different arterial trunks communicate with each other indirectly, is one of the most interesting points in the anatomy of the arterial system. This *anastomosis* of arteries often affords the means of supplying the nutrient fluid to a limb after its principal artery has been obliterated, small collateral channels enlarging more or less for the reception of a greater supply of blood than they were wont to convey. Hence the study of the intercommunicating vessels has had great influence upon the surgical treatment of aneurisms and wounds of arteries.

One of the most simple of these anastomoses is found in the union of two arteries, originating from different trunks, to form one —as the vertebral arteries unite to form the basilar; another kind is when two vessels from the same or different trunks form by their union an arch from the convexity of which others come off, which form similar reunions and arches, giving off smaller branches which

take a similar course, and the arrangement continues to be repeated until the resulting branches are reduced to a very small size, when they pass into the capillary system. This mode of frequent subdivision and anastomosis is seen in the arteries which convey blood to the intestine,—the mesenteric arteries. A third form is where two neighbouring arteries communicate by a distinct vessel, which passes from one to the other. By such vessels the remarkable anastomosis at the base of the brain, the circle of Willis, is formed. The anterior cerebral arteries passing upwards and forwards are united by a cross branch, the anterior communicating artery, and the carotid artery on each side is united to the posterior cerebral artery by a branch which passes from before backwards—namely, the posterior communicating artery. By this free communication of the arteries in front with those behind, and of those on the right with those on the left, the brain is protected against loss of blood, if any of the main channels of its supply should be stopped.

The most common form of anastomosis is found in the limbs. Two principal channels convey blood to a limb, as, in the forearm, the radial and ulnar arteries. The branches of these arteries communicate at various points, especially in the vicinity of the joints, and thus, if any impediment occurs in either, the other enlarges, conveys an increased quantity of blood, and even the obstructed trunk beyond the point of obstruction receives a supply by the anastomosing branches. Or the single main artery of a limb, the femoral, or the brachial, by its branches communicates with arteries which, originating from different sources, pass into another portion of the limb. Thus in the thigh, the circumflex branches of the profunda anastomose with branches which descend from the gluteal, sciatic, and obturator arteries, which are branches of the internal iliac. Hence an obstruction in the femoral, high up, or even in the external iliac, will not deprive the limb of its due supply of blood, for the arteries just named will convey blood to the branches of the femoral, which arise below. This anastomosis may compensate for an obstruction in the internal iliac near its origin, and by a reflux of blood from the femoral through the profunda arteries supply the lower part of that artery. In the treatment of wounded arteries the surgeon must always make allowance for the anastomoses in the neighbourhood of the wound. It rarely happens that a single ligature on the cardiac side of the wound is sufficient to guard against secondary hemorrhage; the anastomotic branches which arise from the main artery above the wound supplying the vessel or its subdivisions below, so that the blood finds

its way by a reflex course to the distal part of the trunk of the artery, and to the wound. This is very apt to occur in wounds of the brachial artery at the bend of the elbow. The only and the obvious method of guarding against such an effect of arterial anastomosis is to apply a ligature to two points of the artery, viz., below the wound, as well as above it.

The supply of blood to various segments of the body through different channels, and the free communication of these channels with each other, must be regarded as one of the most beautiful of the various mechanical contrivances in the human body. By such an arrangement a considerable security is obtained against the failure of the nutrition of the limb by the stoppage of one of its channels. And modern surgery is largely indebted to it for one of its most brilliant triumphs.

The passage of the blood into a limb or organ through various channels serves to distribute it more equally, and to relieve the elementary constituents of the limb or organ from the impetus which the entrance into it of a single large column of blood would occasion. This provision is especially secured for the brain by the subdivision of the four great streams of blood which enter the cranium into several minor ones at the base of that organ, which again undergo extreme subdivision before they penetrate the nervous matter. In animals that hold their heads low the subdivision of the carotid and of the vertebral arteries is very remarkable, and gives rise to the formation of the different kinds of *rete mirabile.* The most remarkable instance of the subdivision of arteries prior to the penetration of the tissue they are destined to nourish is that described by Sir A. Carlisle in the Sloth, which seems to be connected with the extraordinary power enjoyed by those animals of sustaining muscular action for a lengthened period.

The anastomosis of the smaller arterial ramifications are also of great importance in many of the organs and tissues, especially under the skin and mucous membranes. Here a membranous expansion is supplied by a great number of distinct twigs which form a plexus everywhere continuous, and which again gives rise to other smaller plexuses before the ultimate capillaries are given off. To this form of anastomosis of the smaller arteries may perhaps be ascribed the tendency of some inflammations of membranous parts to be propagated rapidly along an extensive surface, as in erysipelas. In some organs, as the kidney, the arterial twigs have no anastomosis whatever.

Of the Veins.—The veins carry the blood back to the heart from

the various tissues and organs. As the arteries divide and subdivide, the veins follow a contrary course. They commence from the capillary plexuses of the tissues and organs by minute radicle vessels, which by their junction form larger ones, and these again unite to form still larger ones; and so by the fusion of the smaller veins larger trunks are produced, until, at length, the venous blood from all parts of the body, is returned to the heart by two great venous trunks, the superior and the inferior *venæ cavæ*.

Veins are much more numerous, and for the most part more capacious than arteries. In the extremities and the trunk they are arranged upon two planes, a superficial plane and a deep-seated one: the latter accompanying the deep seated arteries; the former being immediately subjacent to the skin. The superficial veins are more numerous, and present greater variety both as to number and arrangement, than the deep veins. Their smaller radicles anastomose in the same manner as has been just described in the arteries.

A distended vein has a cylindrical form, which, however, in some is interrupted here and there by a knotted appearance, caused by its enlargement at the situation of its various sets of valves. The coats of veins are essentially the same as those of arteries, but are less developed. Proceeding from without inwards, we find, first, an external tunic, composed of a thin layer of areolar tissue, answering in structure, position, and function to the external coat of arteries. Secondly, we find a fibrous tunic of which the outer portion consists of circular fibres; the inner portion of longitudinal fibres both coarse and fine. The circular fibres are but slightly developed; they are of the same nature as those in arteries and in the larger veins, and exhibit somewhat of the penniform disposition, which we have described in the fibres of the arterial circular tunic. With them are mingled unstriped muscular fibres in less quantity but of precisely the same form and character as those in arteries. In the veins, near the heart, these circular fibres are replaced by similarly disposed muscular fibres of the striped kind continuous with and resembling those of the auricles.*

The longitudinal fibres are well developed, consisting of the outer coarse layer which, in the large veins, as the cava ascendens, are arranged in the form of large bundles, parallel to the long axis of

* Rauschel states that these fibres can be traced in the superior cava, as far as the clavicle, and in the inferior as far as the diaphragm, and in the pulmonary veins as far as the first subdivision of each.

the vessel, and the internal layer or fenestrated membrane which, in every respect, corresponds to the internal longitudinal fibrous layer of arteries. Upon this is placed the epithelium, which is precisely the same as that of arteries.

The imperfect developement in veins of a tunic possessing much elastic power, like the circular fibrous coat of arteries, explains the readiness with which these vessels collapse, and the general thinness of the fibrous and areolar tunics accounts for the diaphanous character of the venous wall.

In a large portion of the venous system peculiar processes, called valves, are found projecting into the interior of the vessel at various points. These processes are semilunar, attached by their convex border to the wall of the vein, and free at their concave border, which is a little thickened. They are disposed in pairs in immediate juxtaposition—sometimes there are three placed together. They are most numerous in the superficial or subcutaneous veins: and are more so in the veins of the lower half of the body than in those of the upper. The smallest veins are destitute of valves; as also are the largest, as the cavæ. The pulmonary veins, those of the liver, and all the veins which contribute to the hepatic portal system, the splenic and mesenteric veins want valves. The renal veins are also devoid of them.

The tissue of which these valves are composed is the same as the longitudinal fibrous coat of the vein, covered by a layer of epithelium; the valves cannot be properly described as reduplications of the inner membrane of the veins, they are processes of it.*

Of the Capillaries.—The system of vessels which is intermediate to the veins and arteries, is called by the name capillary, from the minuteness of their size. The finest arteries, and the finest veins likewise, receive this appellation. But the true capillary system is distinguished by a speciality of arrangement and an uniformity of size, proper to each tissue or organ.

The capillary vessels may be examined in injected specimens, or in recent transparent tissues, as in the pia-mater, or in living transparent tissues, as the web of the frog's foot, the mesentery or distended urinary bladder of the frog, the tail of the newt, the gill of the tadpole, the tail or fins of fishes.

The diameter of the capillaries varies in different textures from

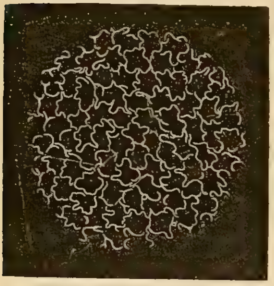
* We have great pleasure in referring to an excellent article on the anatomy of veins in the 42nd part of the Cyclopædia of Anatomy and Physiology, by Dr. S. J. Salter.

the $\frac{1}{1000}$th of an inch, to $\frac{1}{4700}$th, according to the measurements of Weber.

The finest capillaries are found in the brain (fig. 195 A) and in the retina; those of muscles, especially the cross branches which intersect the fibres, are likewise very fine. Among the largest are those of the lung and liver.

The capillaries form a net-work in each tissue or organ, which derives its nourishment directly from them, and they exhibit an arrangement adapted to the disposition of its proximate elements. In the tissues which assume a fibrous form, as muscle, nerve, fibrous tissue, the capillaries are disposed in lines parallel to the fibres, and these parallel vessels are united at variable intervals by cross branches, which pass at right angles to the fibres. (See figs. 47, 95, 161, 162, and 194). In compound or involuted mucous membranes, the capillaries form a plexus with more or less circular meshes, which correspond in form and size to the arrangement of the membrane—good examples of this are found in the mucous membrane of the stomach and of the intestines (fig. 194). When the elements of the mucous membrane are prolonged into processes, forming villi or papillæ, each villus or papilla is found to possess its plexus or system of minute capillary vessels (figs. 161 and 162). In the simple mucous membranes, and in serous membranes, the plexus of capillaries placed in the submucous or subserous areolar tissue exhibits large and irregular meshes.

Fig. 194.

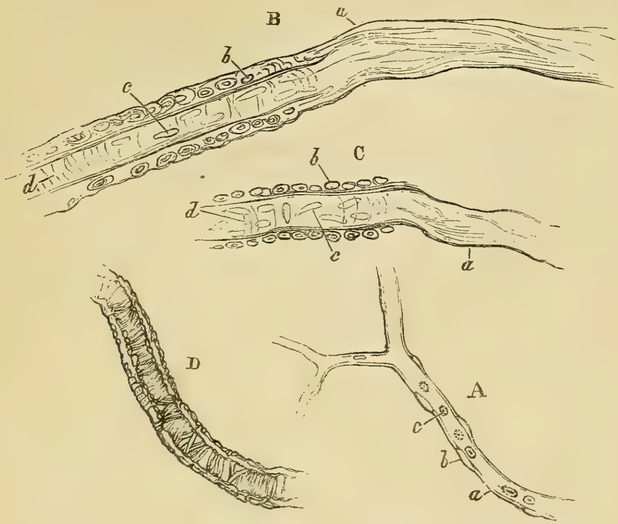


Arrangement of the capillaries on the mucous membrane of the large intestine in the human subject. Magnified 50 diameters.

In the compound tissues the capillaries have no direct relation to the ultimate anatomical elements—that is to say, these minute vessels do not ramify among the ultimate particles of the tissues. It is with their proximate elements they connect themselves. Thus in muscle the vessels lie between the fibres, and are separated from the sarcous particles by the sarcolemma: in nerve, in the same way, they are separated from the nervous matter by the tubular membrane; and in the vesicular matter they play around the vesicles and do not penetrate them. In most of the mucous membranes the basement membrane is placed between them and the epithelium, their nidus being the sub-basement tissue. So, also, with the serous membranes. In bone the finest vessels

are very remote from a large portion of the constituent osseous particles ; ramifying through Haversian canals, they come in contact

Fig. 195.



A. A capillary vessel from the vesicular matter of the human brain. *a.* Homogeneous wall. *b.* Nucleus of the wall. *c.* Red blood-corpuscle.
B, C. Different appearances of small arteries and veins of the human pia-mater. *a, a.* Homogeneous membrane. *b, b.* Circular fibres. *c, c.* Oval nuclei of the internal epithelium, here about to cease. *d, d.* Transverse indications of the circular fibres.
D. Capillary artery from the mesentery of a rabbit. Magnified 200 diameters.

only with the osseous particles of those layers which immediately invest each canal; or with the periosteal or medullary layers. Vessels do not penetrate articular cartilage at all, which must therefore draw its nourishment from the vessels of neighbouring tissues.

The finest capillaries, such as may be most easily examined in connexion with the pia-mater of the brain, appear to consist of a homogeneous tissue, interrupted at short intervals by nuclei which adhere to, or are imbedded in, the wall of the vessel. (Fig. 195 A.) These nuclei are mostly oval—sometimes nearly circular; most of them have their long axes directed parallel to the course of the vessel, but some are placed transversely. In some of these fine capillaries very faint indications of a circular striation may be seen.

In some larger vessels, which perhaps may with more propriety be regarded as capillary arteries, rather than as true capillaries, a distinct arrangement of circular fibres may be seen. These fibres are flat, uniform in diameter, devoid of nuclei, and in all respects, but this, resemble the unstriped muscular fibres.

It had long been a question among physiologists, whether the capillaries had proper walls distinct from the tissues to which they

supplied blood. The microscope has settled this question in the affirmative, for most of the tissues and organs of the body; but it may still be doubted whether the finest capillaries of the liver have walls distinct from those cubical masses of epithelium which they permeate.

Although it is the rule that an intermediate system of vessels exists between the arteries and veins, we find two remarkable exceptions to it. One is in the erectile tissue of the penis; the other in the uterine circulation. In both these instances the arteries communicate directly with the veins. In the penis the ramifications of the arteries pour their blood into the cells of the corpora cavernosa ; in the uterus the small curling arteries of Hunter open directly into large venous sinuses, which in the gravid uterus form an intimate relation of contact with the villous processes of the placenta. These points will be fully described in the chapter on Generation.

It is not improbable that further research may detect a direct communication between arteries and veins, even in tissues, the greatest part of which is furnished with a true capillary plexus. In the cancellated structure of bone and the diploe of the cranial bones, it seems highly probable that the arteries communicate immediately with the veins at many points. Mr. Paget* describes a direct communication between the arteries and veins of the wing of the bat, without any intermediate capillary plexus.†

* Lectures on Inflammation.

† The communication between arteries and veins by capillaries was not known to Harvey. In his time, and for a long period afterwards, anatomists supposed the blood to pass into the parenchyma of the tissues, whence it was received or withdrawn by the veins. Malpighi (about 1687), by microscopic examination, first demonstrated the intermediate capillary system in the lungs and urinary bladder of the frog. Leuwenhoek afterwards (1729) pursued this investigation, and has given some good illustrations of the capillaries examined in transparent parts during life.

Dr. Hales in this country, many years later (1769), gave a very accurate description of these vessels, and denied altogether the idea of the intervention of a parenchyma, or, in his own words, of "glandular cavities." See his Hæmastaticks, p. 146, § 9, vol. ii. W. Cowper, the distinguished myotomist, also made observations on the capillaries of the transparent parts of warm-blooded animals, as the mesentery of a dog, and the omentum of a cat. Haller threw great light upon this subject, and by his facts and arguments settled the question as to the direct continuity of arteries and veins. Subsequently (1745), Lieberkühn advanced our knowledge of the capillaries by his numerous injections, most of which are still extant at Vienna. In more recent times the distinguished Prochaska seems to have been the first to form a just appreciation of the extent of the capillaries, and of their exact relations to the elements of the tissues. His description of the disposition of these vessels, based upon the examination of Lieberkühn's and his own injections, can scarcely be surpassed in the present day. See the 9th chapter (*de vasis saguin. capillar.*) of his Disquisitio Anat.-Phys. Organismi Corporis Hum. ejusque Processus

Of the Heart.—This hollow muscular organ, which, like a forcing pump, drives the blood throughout the vascular system, varies in its constitution, according to the complexity of the circulation, from a simple muscular tube, such as the dorsal vessel of insects, to the complex double heart of man, with its four cavities and its beautiful apparatus of valves.

The dorsal vessel of insects is the most simple condition of the heart. It consists of a muscular tube provided with certain valves, disposed like those of veins; these, by affording an obstacle to the flow of the blood in one direction, determine the course in which it is propelled by the contraction of the muscular wall, namely, towards the head. It is situated along the middle of the back, whence its name. At the points which correspond to the situation of the internal valves, it exhibits distinct constrictions, which in some insects are so marked, that the vessel appears to consist of "a series of slightly conical segments, partially sheathed one upon the other." (Owen.) The blood is propelled to the head through a tubular prolongation of the dorsal vessel, which corresponds to the aorta; this divides into numerous branches, which soon lose themselves in the areolæ, or diffused sinuses, which occupy the spaces between the tissues of the insect; from these sinuses, as from veins, the blood is returned to the heart, and enters that tube at several points, at its posterior, or caudal extremity, as well as at several apertures which are found on each side of the dorsal vessel, near the points of attachment of the valves.

In Crustacea the heart is likewise of a very simple form. In some of the lower Crustacea it is simply a muscular vessel, as in insects; in the higher animals of this class, as in crabs and lobsters, it forms a distinct muscular cavity, or ventricle, giving origin to arteries, and pierced by several venous orifices through which the blood is poured from the large venous sinuses which receive it on its return from the body. It is situated, as in insects, beneath the enlargement of the back.

In the Molluscous classes the heart still retains great simplicity of structure. In the lowest of these, as Tunicata, it is still a muscular vessel, propelling the blood through arteries which ramify on the respiratory organ, whence it is taken up by veins, and returned to the heart. In the compound Ascidians, we meet with the remarkable phenomenon of the oscillation of the currents of the circulation, under the influence of a change in the direction of the peristaltic contractions of the heart.

In the Acephalous mollusks we first observe the subdivision of the heart into two compartments, or cavities; an auricle which receives the blood from the veins and transmits it to a fusiform ventricle which drives it to the various parts of the body. In one of the most highly organized of the Acephalous mollusks, *Venus chione*, Professor Owen describes two auricles, which receive the blood from the veins of the gills, and transmit it to the single fusiform ventricle, which is perforated by the rectum: and in the genus Arca, the ventricle is divided into two cavities, having the rectum in the interspace. An artery is continued from each extremity of the ventricle, which distributes the oxygenated blood over the viscera,

---

Vitalis. Vienna, 1812. Bichat, indeed (1801), had erected these vessels into a system intermediate to that of the arteries and of the veins, but no anatomist who compares the descriptions of the two writers will hesitate to give to the former the merit of a more intimate practical knowledge of the anatomy of these vessels.

the muscular system, and the mantle. The heart of the Gasteropoda, likewise, consists of a single ventricle, which propels the blood to the viscera and the muscular system of the body, and receives it from the branchiæ by one, and sometimes by two, auricles.

In the Cephalopoda, the most highly organized mollusks, the general plan of the heart is the same as in the Gasteropoda. The venous blood is received from all parts of the body by great venous sinuses, which also take up the blood from the gills ; these veins communicate with the heart, which consists of a single cavity, whence arise the two main arteries of the body, called the *superior* and *inferior* aorta.

In Fishes, the heart consists of two cavities ; one, large, loose, and thin-walled, which receives the venous blood—the *auricle ;* the second, thick and fleshy—the *ventricle,* whence an artery springs, the first portion of which, dilated and surrounded by thick muscular fibres, constitutes what is called the *aortic bulb.*

In the Batrachian reptiles there are two auricles, one which receives the blood from the veins of the body—the *systemic auricle ;* the other, which receives it from the lungs, the *pulmonic auricle.* Both auricles communicate with a single ventricle, whence the blood is propelled throughout the body, as well as to the lungs. In Serpents, the heart presents a similar structure ; but in the Python the ventricle is divided by an imperfect septum into two chambers, one of which communicates with the aorta, the other with the pulmonary artery. In the Saurian reptiles, likewise, there are two auricles, and a ventricle, which latter is subdivided into two or more cavities, communicating with each other, and with certain arteries which spring from them—excepting in the American alligator (*Crocodilus lucius*), in which the existence of a perfect septum creates two distinct ventricles.

In Birds and Mammals the heart exhibits its highest developement, consisting, as it does, of two auricles and two ventricles, separated by a complete septum ; each auricle communicating with its proper ventricle, and each ventricle giving rise to an arterial trunk.

The human heart, in the adult subject, occupies an oblique position in the thorax. Its apex is directed downwards, forwards, and to the left side, and in the quiescent state corresponds to the interval between the fifth and sixth ribs. Its base corresponds to the interval between the third or fourth, and the eighth dorsal vertebræ, from which it is separated by the parts contained in the posterior mediastinum. The base of the heart corresponds in front to the sternum at about the level of the cartilage of the third rib.

The weight of the human heart in the adult is about 11 ounces for the male, and 9 ounces for the female (John Reid).

The two great arteries, the aorta and pulmonary arteries, spring from the base of the heart in front. Posteriorly the base is formed by the auricles.

Both the anterior and the posterior surfaces of the heart are divided into two, by means of a groove which corresponds to the anterior and posterior margins of the septum of the ventricles, and which passes from base to apex. The anterior groove contains the left

coronary artery and vein: the posterior the right coronary artery and vein. These are accompanied by nerves. A transverse groove of considerable depth separates the auricles from the ventricles; it contains the coronary vein. All the grooves contain a greater or less quantity of fat, which envelopes the vessels and nerves lodged in them.

Of the four cavities of the human heart, a ventricle and auricle are on each side of the median groove. The ventricles are cone-shaped cavities, their apices being directed towards the apex of the heart, their bases corresponding to the auricles. The left ventricle forms the apex of the heart. When the right ventricle is dilated, its wall extends to, and contributes to form, the apex. Each ventricle, when laid open, exhibits two distinct parts; one, which communicates with the auricle by a large and free aperture, called the *auriculo-ventricular orifice*, through which the blood passes from the auricle into the ventricle; the other, called *the infundibulum*, a funnel-shaped channel, which leads to the artery, and through which the blood is propelled into it from the cavity of the ventricle.

The Valves of the Heart.—The auriculo-ventricular orifice on each side is guarded by certain valves which, when not in action, lie in the ventricle. The valve of the left side consists of two triangular curtains, from the free margin and part of the ventricular surface of which tendinous chords (*chordæ tendineæ*) pass to various points of the wall of the ventricle. The bases of these curtains are attached along a fibrous zone, which separates the auricle from the ventricle. This valve is known by the name of the *mitral valve*, and the orifice is called the *mitral orifice;* the larger curtain is that which separates the infundibulum from the body of the ventricle. The valve at the right auriculo-ventricular orifice, consists of three portions, each having a pointed free extremity extending into the ventricle, and connected to its wall by tendinous cords. Hence this is called the *tricuspid valve.* The base of each segment corresponds to the fibrous zone which intervenes between the auricle and ventricle. Of the three curtains, of which the tricuspid valve consists, the largest is anterior, and the next in size corresponds to the infundibulum of the ventricle.

At each of the arterial orifices of the ventricles there are three valves of semilunar form (Fig. 199), which effectually close the mouth of the artery against the regurgitation of blood into the ventricle. Each of these valves has a convex border attached along the fibrous zone which connects the artery to the infundibulum of the ventricle; and a free concave border divided by a small round body

of fibrous tissue (*corpus Arantii*) into two equal portions. As the blood flows from the ventricle, these valves lie up against the wall of the artery; but immediately the blood regurgitates towards the ventricle, they are pushed by it in towards the mouth of the artery, and their free margins, as well as a considerable portion of their ventricular surfaces coming into close apposition, an effectual barrier is formed against the return of the blood. The semilunar valves of the aorta are essentially the same in all points of form and structure as those of the pulmonary artery; but those of the aorta are the stronger.

The inner surface of the wall of the central cavity of each ventricle is marked by very numerous fleshy columns (*carneæ columnæ*) which project from it in relief. There are three orders of them; first, the simple column in relief, which adheres throughout its whole length to the wall of the ventricle; secondly, the column, attached at each extremity, but free in the interval, so that a probe or other instrument may be passed beneath its middle part; and thirdly, the column attached at one extremity to the wall of the ventricle, and projecting into its cavity by the other: these last are distinguished from the others by the name of *musculi papillares;* the chordæ tendineæ spring from their free extremities, and are inserted into the mitral and tricuspid valves, and one or two into the wall of the ventricle. The infundibular portion of the ventricle is perfectly smooth on its inner surface, and quite free from columnæ carneæ.

The auricles are thin-walled muscular bags of irregular somewhat cuboidal shape. Each communicates by a wide orifice, with its corresponding ventricle, and is separated from its fellow by a thin fleshy septum, which at its middle is so thin as to be translucent. At this situation an orifice existed during intra-uterine life, through which a communication took place between the auricles (*foramen ovale*, or *Botalli*). Each auricle has two distinct portions; the *sinus venosus* which forms by far the greater portion of the bag, and the *proper auricle*, or *auricular appendage*, which appears like an offshoot from the former, somewhat in the shape of a dog's ear, projecting forwards on each side of the aorta and pulmonary artery. The veins pour their blood into the sinus venosus; the auricular appendage receives no blood vessels, but its cavity communicates with that of the sinus venosus. The right auricle receives the two great veins of the system, and the great venous trunk of the heart, the *coronary vein*. The superior vena cava opens into the upper angle of the right auricle, passing downwards and forwards; the inferior

cava opens into its lower angle, passing upwards, backwards, and inwards. The coronary vein opens between the mouth of the inferior cava and the auriculo-ventricular orifice.

On laying open the right auricle, by an incision extending between the two venæ cavæ, an intricate arrangement of muscular bundles called *musculi pectinati*, may be seen on its outer wall. These fleshy columns interlace freely with each other. On the septum a depression exists about its middle, called the *fossa ovalis*, nearly surrounded by a thick fleshy ring called the *annulus ovalis*. This marks the situation of the orifice already alluded to, which existed during intra-uterine life—the *foramen ovale*.

To the left of the orifice of the inferior vena cava there is a valvular process which is another remnant of a mechanism adapted to the circulation through the heart in intra-uterine life. This is the *Eustachian valve*. It is a process of the inner membrane of the auricle, of semilunar shape, which projects between the vena cava and the auriculo-ventricular orifice, and in the fœtus served to direct the ascending current of blood through the foramen ovale into the left auricle. The orifice of the coronary vein is guarded by a small valve called the *valve of Thebesius*. Several small orifices are seen scattered over the inner surface of the right auricle, called *foramina Thebesii*; some of these are the openings of small veins from the wall of the auricle; others merely lead into depressions between the muscular fibres of the auricular wall.

Four veins pour their blood into the left auricle; these are the right and left pulmonary veins, two on each side. The left veins open quite close to each other. The left auricle is placed in the concavity of the aorta, and has lying in front of it the roots of both the aorta and the pulmonary artery.

The inner surface of the left auricle is perfectly smooth, covered with an opaque lining membrane, which appears somewhat thicker than that of the right side. There is no appearance of musculi pectinati in the left sinus venosus; a few, however, exist on the inner wall of the auricular appendage. Here and there some orifices are seen leading to depressions in the wall of the sinus venosus. On the left side of the septum between the auricles we observe traces of the valve-like portions of the septum which formed the immediate boundary of the foramen ovale during fœtal life.

Of the Pericardium and Endocardium.—The heart is enclosed in a fibrous bag, the fibrous pericardium, which is closely adherent below to the central tendon of the diaphragm, and above becomes continuous with the external tunic of areolar tissue, which invests

each of the large arterial and venous trunks that connect themselves with the heart. This bag serves to fix the position of the heart, and to prevent any sudden or extensive displacement, which might interfere with its proper action. It consists almost exclusively of white fibrous tissue.

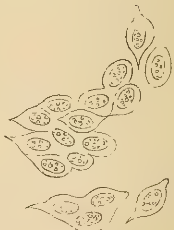
Within this fibrous bag is a serous membrane, *the serous pericardium*, which resembles in all points of arrangement and structure the other membranes of its class. One portion of it invests the internal surface of the fibrous pericardium, while the other covers the heart, the line of reflection passing over the great vessels at the base of the heart.

The cavities of the heart are lined by the endocardium, a membrane continuous with and closely similar to the lining membrane of arteries and veins. It consists of a layer of epithelium placed on a stratum of fine fibres which exhibit minute wavings. The epithelium appears to be extremely delicate, but the same in all its characters as that of the blood-vessels. It is so delicate that to be seen satisfactorily it must be examined in animals

Fig. 196.

Epithelium from the left auricle of the horse (magnified 200 diams.) showing the two forms of particles, the round and the pointed.

Fig. 197.



Epithelium from the left ventricle of the horse (Magnified 200 diams.).

just killed. We observe two forms of epithelial particles, one soft, rounded and globular, the other somewhat compressed and drawn out at opposite poles into pointed or fibre-like processes. (Fig. 196.) It is difficult to determine the precise relative position of these two forms of epithelium, but it seems probable that the pointed processes are the more deeply seated, and are in immediate contact with the subjacent fibrous layer, which here corresponds to the basement membrane beneath the epithelium of serous and mucous membranes.

The endocardium of the left auricle, and of the septum and auricular appendage of the right auricle, is thicker and denser than

that in other parts of the heart. This is due to an increased developement of the fibrous layer beneath the epithelium, especially of its yellow element. The precise meaning of the greater thickness of endocardium in these parts of the heart is far from obvious.

Of the Structure of the Valves of the Heart.—The valves of the heart are formed by processes of fibrous tissue covered by epithelium. Between the auricle and ventricle, as well as at the mouths of the aorta and the pulmonary artery, there are remarkable developements of fibrous tissue. Interposed between each auricle and ventricle there is a fibrous zone or ring, to which the muscular fibres of the auricle adhere on the one hand, and those of the ventricle on the other. The fibrous tissue is prolonged inwards towards the cavity of each ventricle, so as to form three curtains on the right side (the tricuspid valve), and two on the left (the mitral valve). These curtains are continuous with the chordæ tendineæ, which appear to be inserted into them at their margins and at various distances from them on the surface next to the ventricle, but not at all on that which corresponds to the auricle. They are covered on both surfaces by epithelium, which likewise extends over each of the chordæ tendineæ. The fibrous tissue at the orifice of the pulmonary artery, as well as at that of the aorta, consists of fibrous cords arranged as three festoons continuous with one another, the convexity of each being directed towards the muscular tissue of the infundibulum of the ventricle, and its concavity to the artery. On the right side the muscular fibres of the infundibulum adhere to a small portion of the centre of the convexity of each of these festoons, and the circular fibrous coat of the artery seems closely attached to the whole extent of the concavity. On the left side, the fibrous festoons are connected partly with the muscular fibres of the ventricle, and partly with the base of the inner curtain of

Fig. 198.

A portion of the aortic semilunar valve in the dog. *a*, Surface of the valve. *b*, Nuclei of the epithelium seen on its margin.

Fig. 199.

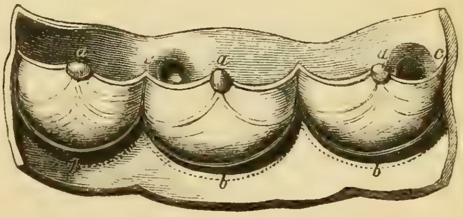


Diagram of the semilunar valves of the aorta (after Morgagni). *a*, Corpus Arantii on the free border. *b*, Attached border. *c*, Orifices of the coronary arteries.

the mitral valve. The process of fibrous tissue extends from each festoon towards the mouth of the artery, forming a loose semilunar curtain, which is the basis of the valve. Each of these curtains presents a convex attached border, and a concave free border, interrupted at its middle, or bisected so as to form two concave borders, by a slight thickening of the fibrous tissue, which forms a small spherical body called the *corpus Arantii;* it also has a convex surface directed towards the ventricle, and a concave surface directed towards the artery. The bundles of fibres which constitute this fibrous basis of each valve are disposed in festoons, some parallel to the fibrous festoon of the attached border; others, and the greatest number, parallel to the smaller concave borders on each side of the Corpus Arantii. The fibres nearest the attached border of the valve are considerably more developed than those near its free margin. Indeed, for a space of about three or four lines from the edge of the valve the fibrous tissue is extremely thin and almost transparent. It is at this part of their ventricular surface that the valves come in contact when they close the arterial orifices, forming a mutual support to each other, and leaving the main stress of the backward pressure of the column of blood in the artery, to be borne by that portion of each valve which intervenes between this and its attached border. Hence the greater thickness of the fibrous basis in this situation. It is worthy of notice that the tissue of the endocardium is nearly, if not completely identical with the inner longitudinal fibrous tunic of arteries; a fact which explains the close similarity between the diseased states of the arterial tissue and those of the endocardium and the heart's valves.

Fig. 200.

Fibrous tissue of a semilunar valve beneath the endocardium.

Mechanism of the Valves.—The valves are closed by the mere hydraulic pressure of the blood. When the blood accumulates in the ventricles, it pushes up the auriculo-ventricular valves towards the auricle until their several portions come in contact with each other, and close the orifice. But the simple contact of the curtains of these valves with each other would not prevent regurgitation; for the same hydraulic pressure which brings them in contact would push them into the auricle, were it not that their margins are connected with the walls of the ventricle and the musculi papillares by means of the chordæ tendineæ. When the ventricle contracts, it draws

firmly by means of the chordæ tendineæ upon the valves, and not only keeps them closed, but causes them to exercise a considerable pressure on the blood, which promotes its onward flow into the artery.

Thus, by the attachment of the chordæ tendineæ to the several curtains of the valves, not only is regurgitation of the blood opposed, but every part of the surface of each curtain is made to press upon the blood with a force equal to that of the contraction of the ventricle, and to aid in propelling it through the artery. Should, however, any imperfection of the valve exist, as by the imperfect apposition of its several portions, a chink remains between their margins, and regurgitation takes place to a degree proportionate to the size of the chink.

The semilunar or arterial valves are closed in their turn by the pressure of the blood from the artery backward towards the heart. The blood forcibly driven back by the elastic reaction of the arterial walls, slips between the wall of the artery and the valves, at the sinuses of Valsalva, and throws the latter inwards, causing them to meet and close the arterial aperture, thereby preventing regurgitation into the ventricle. Thus the force by which the arterial valves are closed, being the elastic reaction of the arterial walls, excited by the expulsive force of the ventricle, bears a constant ratio to the contractile power of the wall of the heart, and, therefore, the degree of tension of the semilunar valves, and the sound which it developes (the second sound of the heart) enables us to form an estimate of the expulsive force of the ventricle, which is often of great value in practice.

Of the Muscular Tissue of the Heart.—The heart is composed of muscular fibres of very various sizes. In all essential points of structure these fibres resemble very closely the striped fibres of the external muscles, differing from them, however, in the extreme tenuity of the sarcolemma. They interlace with each other in an intricate manner, and assume opposite directions on different planes, thus forming a complicated interlacement of fibres, which adds greatly to the power of resistance possessed by the organ. By this interlacement the fibres of the heart adhere to each other, for between them there is little or none of that areolar tissue which exists in considerable quantity in the external muscles, and unites their fibres and fascicles together. This interlacement takes place irrespective of any subdivision of the fibres. Nevertheless, it has recently been noticed by Kölliker and other good observers, that a true anastomosis does take place between adjacent fibres by the

branching of each fibre, and the fusion of neighbouring branches. A somewhat similar branching and anastomosis of the ultimate muscular fibre has been observed at the surface of the tongue, an organ of which the muscular structure is not unlike that of the heart.

The complicated disposition of the fibres of the heart on different planes has, no doubt, the object of strengthening the walls of its cavities, and insuring a uniformity and synchronousness in the contraction of all its fibres. This arrangement belongs particularly to the ventricles, where such a mode of action is most needed. It may be best demonstrated on hearts which have been subjected to long boiling. By this process the fibre is hardened, and may be readily torn in the direction of its course, and thus, by a little careful manipulation, the connection of the fibres and bundles of fibres may be unravelled.

The ventricles are covered by a thin layer of fibres common to both. These may be traced, apparently emerging from the apex and spreading out over the anterior as well as the posterior surface of the heart. At the apex these fibres pass in to form a connection with the fibres which form the innermost layer of the wall of each ventricle; from the same point these superficial fibres pass obliquely, those of the posterior surface from right to left; those of the anterior surface rather in the direction from left to right. At the transverse fissure they sink in to attach themselves to the fibrous zone which separates auricles from ventricles. According to some anatomists (Reid and others), many of the superficial fibres do not pass beyond the anterior longitudinal fissure, but sink into and become incorporated with those of the septum.

If the fibres of the apex be traced inwards, they are found to penetrate so as to form the innermost layers of the walls of the ventricle, contributing likewise to form the carneæ columnæ, and becoming attached to the fibrous structures of the ventricle, both to the chordæ tendineæ and the auriculo-ventricular zone. Some of these fibres serve to connect opposite walls of the heart: thus the deep layer of fibres of the posterior wall of the heart receives fibres from the superficial layer of the anterior wall, and reciprocally the superficial layer of the posterior wall contributes to the deep layer of the anterior. But others of the superficial fibres are continuous with the deep fibres of the same wall. These are the fibres which in passing from the superficial to the deep portion of the wall, make a remarkable turn in figure of 8, of which the lower portion is very small, as described and figured long ago by Lower.

Between the superficial and the deep or reflected portion of the ventricular fibres are some which have been described as the proper fibres of the ventricles; these pass round each ventricle in a circular direction, some obliquely, some at right angles to its axis; they form a sort of hollow cylinder for each ventricle, which is attached above to the fibrous zone of the auricles, and is open below towards the apex. On the right side a smaller number of circular fibres embrace the infundibular portion of the ventricle, attaching themselves to the fibrous festoons of the pulmonary artery.

Of the Muscular Fibres of the Auricles.—In the auricles we find a common and a proper set of fibres. The former may be traced along the anterior surface of both auricles, embracing them like a belt, but not extending round to the posterior surface. The latter are arranged in several circular or spiral bands, some of which spring from the auriculo-ventricular zone, and return to it again, and envelope the auricle before and behind, passing sometimes at right angles to it, sometimes obliquely; others pass round the auricle in a horizontal direction and parallel to the auriculo-ventricular zone. Each of the venous orifices of the auricles is surrounded by a series of circular fibres (sphincter-like) which are continued, as already referred to, to a considerable distance along the trunks of the veins, retaining in this latter situation just the same character as at the auricle itself. This is a good situation for seeing the branching and anastomosis of the fibres.

Nutrition of the Heart.—The heart is nourished by blood derived from the aorta. Its arteries, the right and left coronary arteries, are the first branches which spring from the aorta. They leave that vessel just beyond the margins of the semilunar valves. The right passes along the circular groove between the auricles and ventricles, and sends a branch down the posterior median groove to the apex; the left passes along the anterior median groove, anastomosing at the apex with the latter branches. Corresponding with the small size and the oblique direction of the heart's fibres are an extreme closeness and an everywhere oblique sloping of the capillary network. From this, venous radicles are formed at various points and unite into large veins which are found in the grooves of the heart accompanying the arteries; these veins terminate in the coronary vein, which is lodged in the right portion of the circular groove, and opens into the right auricle close to the orifice of the inferior vena cava.

Nerves.—The nerves of the heart are derived from the cardiac branches of the pneumogastric nerve, and from the sympathetic.

These nerves form by their frequent anastomosis a plexus called *the cardiac plexus.* It is situated upon the aorta and pulmonary artery, just as they have issued from their respective ventricles, and is commonly described as consisting of two portions—*the superficial cardiac plexus*, which corresponds to the concavity of the arch of the aorta, and lies in front of the right branch of the pulmonary artery; and *the deep cardiac plexus*, which is much the larger portion, and lies behind the arch of the aorta between it and the bifurcation of the trachea. To the formation of these plexuses, branches derived from the vagus and the sympathetic on both sides contribute.

The greatest part of the nerves which emanate from these plexus entwine around and accompany the right and left coronary arteries, forming the anterior and posterior coronary plexuses. From these, nerves pass to the auricles and ventricles, but chiefly to the latter. A ganglion, described first by Wrisberg, and called after him *ganglion cardiacum Wrisbergii*, is generally found in front of the left auricle, and behind the aorta. Scarpa has also described gangliform enlargements of the nerves on the anterior surface of the ventricles, to one of which, situated on the anterior surface of the horse's heart, half-way down the anterior groove, he refers under the name of "cardiaci sinistri ganglion insigne."* It is probable, however, that none of these latter enlargements are truly ganglionic in their nature.

Remak describes numerous microscopic ganglia on the nerves of the heart of the calf. We have seen some of these small ganglia upon the surface of the auricles in the calf's heart, although we have not succeeded in detecting them on the surface of the ventricles, nor in the substance of the septum, as delineated by Remak. We can vouch for the truly ganglionic nature of those which we have seen from the unequivocal existence of vesicular matter in them.†

Some elaborate dissections of the nerves of the heart have lately been made by Dr. Robert Lee,‡ from which it appears that the heart is more largely supplied with nerves than had been hitherto supposed, and that a larger number go directly to the muscular structure of the heart, independently of the arteries, than had been admitted by previous anatomists. Upon these nerves numerous

* Scarpa, Tabulæ Anatomicæ. Ticin. 1794. Tab. vii. fig. 1.

† Remak, Neurologischen Erlauterungen. Muller's Archiv. 1844. Tafel xii.

‡ Phil. Trans. 1849.

gangliform enlargements may be seen which Dr. Lee figures as of great size upon the nerves of the posterior surface of the heifer's heart.

Our own dissections* enable us to confirm the general accuracy of Dr. Lee's delineations, although we have not discovered so many nor such large nerves as he depicts. We have likewise seen numerous swellings on these nerves, which again we have failed to find, either in such numbers or of the same size as those represented in Dr. Lee's plates.

The nerves are composed altogether of gelatinous fibres, and the swellings do not contain vesicular matter; and, therefore, do not partake of the nature of ganglia. As filaments invariably pass from these swellings into the muscular structure of the heart, we would regard them as resulting from that loosening of the constituent fibres of nerve trunks which invariably takes place just before branches are given off from them.

Of the Action of the Heart.—The action of the heart is remarkable for its rhythmical character. Each of its cavities exhibits a succession of contractions and dilatations following each other with the most perfect rhythm. Cavities of the same kind contract or dilate simultaneously; but the ventricles are in contraction or *systole* when the auricles are in dilatation or *diastole*, and *vice versâ*. Following the course of the circulation through the heart, the auricles having been filled from the veins which open into them, contract and expel their blood into the ventricles, which, in their turn, contract to drive the blood into the arteries. When the ventricles contract, the heart experiences a peculiar tilting movement, by which its apex is raised from the level of the sixth rib to the space between the fifth and sixth, and at the same time it is rubbed more or less forcibly against the wall of the chest. The wall of the ventricles is firmly contracted at every point, and rendered hard and tense; and, therefore, in its movement it communicates a considerable vibration to the wall of the chest, giving rise to what is called the *impulse*. This impulse is caused altogether by the systole of the ventricles and the consequent movement of the heart; it is always directly proportionate to the size of the ventricles, or to the extent of their surface in contact with the wall of the thorax, and to the vigour of their contractions. According to Valentin's experiments the tilting movement of the heart will take place even when the apex has been cut off,

* We take this opportunity of acknowledging the valuable assistance of our friend and pupil Mr. Samuel Martyn in these dissections.

denoting that that phenomenon cannot be due to any recoil consequent upon the resistance to the passage of the blood through the great vessels, and that its true cause is the contraction of the fibres of the ventricle.

Certain sounds accompany the heart's action, the accurate interpretation of which has shed a flood of light upon the diagnosis of diseases of that organ. On placing the ear over the region of the heart in a healthy individual, the following phenomena may be perceived; first, a heavy, somewhat prolonged sound, which is synchronous with the impulse, and is best heard over the heart's apex; this is the *systolic* or *first* sound; secondly, a short clicking sound immediately succeeding this; it is synchronous with (but not caused by) the diastole of the ventricles, and is called the *diastolic*, or second sound; it is best heard over the base of the heart near the root of the aorta. After this the heart seems to pause, as it were to take rest, and then follows the first sound again, followed instantly by the second sound, and then the pause. The duration of the first sound is about double that of the second, while that of the second is equal to the pause. Thus if the whole period of the heart's action be divided into four parts, the first two would be occupied by the first sound, the third by the second sound, and the fourth by the pause.

Numerous experiments and observations have been made with reference to the question of the signification of these sounds. We must here content ourselves with stating the conclusions which we think may be safely drawn from them. The first sound is composed mainly of the muscular sound generated by the contraction of the ventricles, strengthened by that due to the sudden tension of the auriculo-ventricular valves over the blood contained in the ventricles, this tension being effected by the contraction of the carneæ columnæ, which is synchronous with that of the rest of the ventricular wall. To these causes of sound may be added the impulse of the heart against the wall of the chest, and, perhaps, also the collision of the blood against the orifices of the great vessels.

The second sound is due to the sudden tension of the semilunar valves of the two great vessels by the recoil of the columns of blood injected into them by their respective ventricles. An experiment, originally suggested by the late Dr. Hope, and repeated by several observers, proves this unequivocally. If in an animal whose respiration is maintained by artificial insufflation, the heart's action being thereby prolonged, a hook be introduced into the aorta so as to hold back one of its valves, and leave a passage for

the regurgitation of a portion of the blood after each systole of the ventricle, a bellows sound becomes generated which usurps the place of the clicking second sound. But the moment the valve is allowed to resume its play, the natural click returns.

That this is the correct interpretation of the sounds of the heart, is further proved by the observation of the influence of various morbid states of that organ upon them. Thus the first sound is modified by whatever increases or weakens the intensity of the ventricular systole, of the impulse, and of the tension of the auriculo-ventricular valves; and when the latter takes place imperfectly by reason of the insufficiency of the valves to close the orifices, the first sound is accompanied (not replaced) by a bellows sound due to the regurgitation of blood from ventricle to auricle. Again, should one or more of the semilunar valves be so injured or altered as to prevent the complete closure of the arterial orifice, at the time of the diastole, the second sound is replaced by a bellows sound, just as in the experiment above detailed.

The regular succession of the two sounds and the pause, bearing to each other the relative duration already mentioned, constitutes the rhythm of the heart.* Sometimes the pause lasts for a much longer period than a fourth of the whole, for as long or longer than would suffice for the developement of the other two sounds. Under these circumstances the heart is said to intermit, and its rhythm is interrupted.

At every systole of the heart an impulse is felt in all the large arteries of the body, which is synchronous with the contraction of the ventricles, or so nearly that the difference is inappreciable except in very distant arteries as those of the tarsus. This impulse in the arteries constitutes the pulse—which will be fully described by and by (p. 353), and which, from its general accordance with the heart's action, affords the readiest means of judging of the heart's rhythm, and counting the frequency of its action.

When the rhythm of the heart is regular, this succession of first and second sound (systole and diastole) and pause may be heard a certain number of times in a minute in each individual, and by a series of observations, the scale may be formed shewing the average frequency of the heart's action at different periods of life in man. This is shewn in the following table, which is that formed by our able friend and colleague, Dr. Guy, from a comparison of numerous observations.†

* Some observers admit the existence of a short pause after the first sound.

† Art. *Pulse*, Cycl. Anat. and Phys.

TABLE OF THE AVERAGE FREQUENCY OF THE HEART'S ACTION AND OF THE PULSE AT DIFFERENT AGES.

At birth	140
Infancy	120
Childhood	100
Youth	90
Adult age	75
Old age	70
Decrepitude	75—80

In general the frequency of the heart's action and of the pulse in the female exceeds that of the male, after the seventh year; if the average pulse of the adult male be stated at 70, that of the adult female may be put down at 80.

The heart's action is seldom less frequent than 45 or 50 in health; Heberden has counted it as low as 42, 30, and even 26 in healthy males; and Fordyce counted it in one case 26 in an old man, and in another 20. In cases of chronic disease of the brain it falls very low. We have ourselves counted it as low as 16 in one of these cases for months together.

According to the researches of Drs. Knox and Guy, the frequency of the heart's action (and the consequent frequency of the pulse) varies at different periods of the day. It is most frequent in the morning, and becomes gradually slower as the day advances. The diminution is most marked at night.*

Posture exercises a remarkable influence on the frequency of the heart's action. The law is that the frequency is the greatest in the erect position, next to that, in the sitting, and least in the horizontal posture. The following table has been framed by Dr. Guy from the results of sixty-six observations in the male, and twenty-seven in the female.

TABLE OF THE FREQUENCY OF THE HEART'S ACTION IN DIFFERENT POSTURES.

	Standing.	Sitting.	Lying.	Differences.
Males	81	71	66	10, 5, 15
Females	91	84	80	7, 4, 11

These observations denote the curious fact that posture influences the frequency of the pulse less in the female than in the male, and from another series of more numerous observations, Dr. Guy deduces that the effect of change of posture on the frequency of the heart's action in the male, is more than twice as great as in the female.

* See Graves's Dub. Hosp. Rep., vol. vi., and Dr. Guy's art. *Pulse,* Cyclo. Anat. and Phys.

The cause of this difference in the frequency of the pulse in different postures resides probably in the effort employed to maintain the muscular contractions necessary to support the erect or sitting postures. But careful experiments are still wanting to ascertain whether a simple difference of posture, without muscular exertion, would develope a change in the frequency of the pulse. Those as yet done by the revolving board, seem to have had reference only to the exertion of muscular force in the production of the *change* of posture, and not to that required for the continued effort to maintain the attitude.

The Course of the Circulation in the Adult.—Taking the left ventricle as the starting point for the circulation, we may describe the blood as pursuing the following course. By the left ventricle it is driven through the aorta into every artery of the body save the pulmonary; and having passed through the capillary system it enters the venous radicles, and from them it passes to the venous trunks; it is at length returned by two great trunks, the superior and inferior *venæ cavæ* to the right auricle of the heart. This portion of the circulation, from its traversing the whole system, except the lungs, and from its occupying by far the largest part of the body, is called the *systemic* or *greater* circulation. The venous blood, brought by the great venous trunks to the right auricle, is expelled by that cavity into the right ventricle, which drives it by the pulmonary artery through the lungs to the pulmonary veins, through which it passes to the left auricle, and so on to the left ventricle. This portion of the circulation, traversing only the lungs, and connecting the right ventricle and left auricle, forms the *lesser* or *pulmonic* circulation.

Of the Portal Circulation.—In general the arterial blood passes through a single system of capillaries and veins before it is returned to the auricle. But there are two remarkable exceptions to this — one in the portal circulation of the liver, the other in the kidneys. In both these cases the blood passes through two subsystems of capillaries after it leaves the arteries. Thus, as regards the hepatic circulation, the blood conveyed to the intestines by the arteries, passes through the intestinal capillaries into the intestinal veins, whence it passes to the trunk of the vena portæ, which again transmits it to the hepatic capillaries, and thence to the hepatic veins, through which it reaches the heart. A portion of the circulation, of which the chief vessel is formed like a vein, and distributes its blood like an artery, is called a portal circulation. A similar circulation is found in the kidneys. The afferent arteries

end in the Malpighian tufts, whence the blood is taken up by the efferent veins, which quickly break up like arteries into another capillary plexus surrounding the uriniferous tubes, and this plexus gives origin to the radicles of the renal or emulgent veins.

The hepatic portal circulation, however, has several points of communication with the systemic veins or the inferior vena cava; and thus it happens, when from disease of the liver a considerable portion of the portal system of that organ is obstructed or obliterated, that a part of the blood from the intestinal canal finds its way into tributary veins of the cava, and returns by that route to the right side of the heart. The points of communication are between the veins of the cava (left renal) and of the intestines, especially the colon and the duodenum, and between the inferior mesenteric and the hemorrhoidal veins, a fact which explains the frequent occurrence of hemorrhoids in obstructions of the liver; also between superficial branches of the portal veins of the liver, and the phrenic veins, as pointed out by Kiernan.

Bernard states that immediately after the portal vein has entered the liver, and sometimes before, a certain number of branches are given off from it, which, entering the liver, some superficially, others more deeply, form communications with the vena cava.

Of the Fœtal Circulation.—In the fœtus in utero the course of the circulation is greatly modified, by reason of the inaction of the lungs as aërating organs, and the consequent imperfect attraction of the blood to them. During intra-uterine life, the aëration of the fœtal blood is effected by the placenta, a highly vascular organ, in which the fœtal blood is brought into a very close relation to the maternal blood as it circulates through the wall of the uterus. The placenta, therefore, is in effect the lung of the fœtus, and bears a corresponding relation to its circulation.

A large portion of the fœtal blood is carried to the placenta through the umbilical arteries, which are continuations of the trunks of the internal iliac arteries escaping from the body of the fœtus through the umbilicus. From the placenta the blood is returned to the fœtus by the umbilical vein, which is bound up with the umbilical arteries in the umbilical cord, and enters the body of the fœtus at the navel. From this point the umbilical vein passes upwards and to the right side under the liver, in its longitudinal fissure, and at its transverse fissure it joins the sinus of the vena porta, through which most of its blood is distributed to the liver. One large branch, however, follows the course of the original trunk in the posterior part of the longitudinal fissure, and opens

into the inferior vena cava, just before that vessel communicates with the heart. This vessel is the *ductus venosus*—a continuation of the trunk of the umbilical vein—through which some of the blood returning from the placenta, passes directly to the inferior vena cava, and to the right auricle of the heart, without traversing the liver.

The blood thus received from the inferior vena cava (being that from the body below the diaphragm), and also from the placenta, does not pass into the right ventricle. A very interesting piece of mechanism obstructs its passage in that direction, and favours its flow across the right auricle through the foramen ovale, now freely open in the septum, into the left auricle. This is the Eustachian valve, which is situated between the inferior vena cava and the right auriculo-ventricular opening, and being connected with the anterior and inferior part of the annulus ovalis, it brings the foramen ovale into very close connexion with the inferior vena cava, and forms an imperfect septum towards the auriculo-ventricular opening, quite sufficient, however, to impede the flow of blood in the downward direction.

Arrived in the left auricle, the blood is transmitted thence to the left ventricle, and from this latter cavity through the arch of the aorta to the head, neck, and upper extremities, whence it is returned by the venæ innominatæ and by the superior vena cava to the right auricle, which transmits it to the right ventricle. This latter ventricle propels it into the trunk of the pulmonary artery, which in the fœtus, divides into three vessels, not into two, as in the adult. These are the two pulmonary arteries which separate from the trunk at right angles, one for each lung, and between them, following the direction of the parent trunk, a large vessel, nearly as large as the pulmonary artery itself, which forms a direct anastomosis with the aorta, just below its arch. This is the *ductus arteriosus*, through which the blood is transmitted directly from the right ventricle to the commencement of the abdominal aorta.

Of the Forces by which the Blood is circulated.—The principal force by which the blood is moved throughout the vascular system, and returned to the heart is that which is generated by the contraction of the left ventricle, or what is commonly called the *vis a tergo* of the heart.

The force with which the heart propels the blood into the arterial system has been variously estimated. Valentin considers that the left ventricle exerts a force equal to one-fiftieth of the weight of the body, and taking the muscular power of the right ventricle

to be half that of the left, he would estimate the power of the latter at one-hundredth part of the weight of the body. This would give a force of upwards of three pounds for the left ventricle for a man weighing eleven stone, and half of that for the right.

Now Hales had long ago (1769) shown that under the pressure of a column of water nine feet and a half in height, fluid might be made to pass from the carotid artery to the jugular vein through the capillary system. And it is well known to anatomists that when the vessels are free from coagulated blood or other mechanical obstruction, thin fluids may be transmitted by a very slight force from the arteries to the veins.

Dr. Sharpey's experiments * indicate the exact amount of force necessary for this purpose. A syringe with a hæmadynamometer, to show the amount of pressure used, was adapted to the thoracic aorta of a dog just killed, the abdominal aorta having been previously tied immediately above the renal arteries, and the inferior vena cava opened just as it passes through the diaphragm. Fresh defibrinated bullock's blood was injected with a pressure of three and a half inches of mercury, and passed through the double capillary system of the intestines and the liver out of the veins with a full stream. When the pressure was increased to five inches, the blood spirted from the vein in a full jet. When the aorta was not tied above the renal arteries, the same pressure sufficed to drive the blood through the vessels of the lower extremities, and it was made to traverse the capillary system of the lungs by a pressure of from one and a half to two inches of mercury, so as to flow freely through the pulmonary veins. Allowing one pound for every two inches of mercury, it would thus appear that a pressure of two pounds was sufficient to complete the circulation through the two abdominal capillary systems—and of one pound for the pulmonary circulation.

Unless, then, we assume that there are obstacles to the flow of blood through the vascular system, which during life are much greater than those after death, it must be granted that the heart's force, which in man does not probably exceed three pounds, is sufficient to drive the blood throughout the three systems of blood-vessels, and to maintain the current of the circulation; and that this force alone is capable of producing all the grand phenomena of the circulation.

It remains, then, to inquire whether the *vis a tergo* of the heart is the sole force by which the circulation is maintained, or whether

* See Williams's "Elements of Medicine," p. 185.

we must not seek for the operation of other forces in order to explain its phenomena. To determine these points we must investigate the phenomena of the circulation in each of the systems of blood-vessels, and first in the arteries.

Phenomena of the Circulation in the Arteries.—By each contraction of the left ventricle a certain quantity of blood is pumped into the arterial system which is already full. Were the arteries and other blood-vessels a series of rigid and inelastic tubes there would necessarily ensue upon this a discharge of blood, corresponding in quantity and rapidity, from the opposite extremity of the system. It is plain, however, from the slow rate of the venous circulation, and the less capacity of the auricles as compared with the ventricles, that this does not take place in the vascular system; nor considering the great extent of surface which the blood has to travel over in the capillaries, and the consequent friction it has to encounter, can it be expected that a quantity of blood should be discharged into the capillaries equal to that which the heart injects into the arteries.

Room is obtained for each fresh quantity of blood (beyond that which can be simultaneously expelled from the opposite extremity of the vascular system) by the dilatation of the arteries under the force of the heart. The eminently extensible and elastic character of the arterial walls thus gives a peculiar feature to the arterial circulation, and is turned to good account in maintaining the flow in that system of blood-vessels. In yielding under the force of the heart the arteries become dilated at each systole to the extent, according to the experiment of Poiseuille upon the carotid of a horse, of one-twenty-third of its diameter, or of one-twenty-second, in a similar trial by Valentin on the carotid of a dog; but which must vary in different arteries and at different times with the force of the heart, and the extensibility of the arterial wall. Poiseuille's observation, however, pointed out unequivocally the fact (previously doubted), that the arteries are dilated at each systole of the heart.*

This dilatation of the arteries calls into play a force which in some degree replaces the heart's force. The elastic arterial wall, stretched by the contraction of the heart, reacts with a power which approximates more closely to that by which it was dilated according as the arterial tissue is more or less elastic. The arteries are thus made to contract upon their contained blood, and to drive it

* See the account of Poiseuille's experiment, and a figure of his instrument in Majendie's Journal, tom. ix., and also in Valentin's Physiologie, Bd. i. p. 449.

onwards or from the heart, and backwards or to the heart. Its course, in the latter direction, is speedily checked by the sudden and forcible closure of the aortic valves under the pressure of the regurgitating current. Therefore, the great mass of the blood rushes onwards towards the capillary system,—propelled first by the heart's impulse, and, secondly, by the elastic reaction of the arterial walls.

This elastic reaction of the parietes of the arteries does not come into play until the heart has ceased to contract and begun to dilate. It is, therefore, synchronous with the diastole of the heart, and corresponds with it in duration; so that while the ventricle is inactive the blood in the arteries is still being pressed upon by the reacting arterial walls. Thus the blood is ever moving onwards throughout the arterial system, during the diastole, as well as during the systole of the heart; and the jerking impulses communicated to it by the successive contractions of the ventricle are gradually converted into that continuous uniform forward movement, which is observed under ordinary circumstances in the ultimate arterial ramifications, the capillaries and the veins.

An analogous application of the reacting force of an elastic agent to convert a jerking movement into a continuous stream is found in the mechanism of the fire-engine, and of the organ. In the one water, in the other air, is forced into a chamber in which air already exists. This air undergoes compression by the sudden introduction of a new quantity of water or air. Its elasticity causes it to react, and thus to supply an expulsive force during the subsidence of the action of the piston in the one case, and of the bellows in the other.*

The heart, by its propulsion of blood into the arterial system, not only dilates the arteries, but elongates them likewise. This is generally better seen than their dilatation, but it is most apparent in arteries which are curved. Under the influence of the heart's

* This explanation of the influence of the elastic reaction of the arterial wall in promoting a continuous stream, and converting the jerking current of the blood in the large arteries into a uniform one in the small ones is very commonly attributed by modern writers to Weber. English physiologists ought not to have overlooked John Hunter's remarks (on the Blood, &c. 4to ed. p. 129,) nor Sir C. Bell's observations in his "Animal Mechanics," p. 44. But the following passage from Hales will show that that able observer held much the same views long prior to either of those last named. * * * "The blood in the arteries," he says, "being forcibly propelled forward, with an accelerated impetus, thereby dilates the canal of the arteries, which begin again to contract at the instant the systole ceases: by which curious artifice of nature, the blood is carried on in the finer

systole the curves are distinctly altered so as to form segments of larger circles, a motion is communicated to the artery, and a change of place results; and straight arteries, which are more or less confined by the superjacent parts, become slightly curved under the same force. Thus, in the course of time, the arteries, especially those of parts to which by reason of a more active nutrition in them there is a considerable afflux of blood, assume a tortuous form, as may be seen in the temporal and radial arteries of old persons, and in the spermatic artery of the bull.

The Pulse.—When the finger is applied to an artery during life, it is felt to beat or pulsate in correspondence with the systolic actions of the heart, so that the number of pulsations in the artery corresponds exactly with the number of beats of the heart, and if an occasional interruption in the heart's action take place, or what is called an intermission, there will be at the same time a failure in the beats in the artery.

This phenomenon is called the *pulse.* From their contiguity to the heart it is always present in arteries, but it may occur in veins under circumstances to be explained hereafter. It is due to the same cause, which occasions the blood to flow *per saltum*, or by successive jets, from a divided artery. That cause arises out of the manner in which blood is pumped into the arterial system by successive jerks. Each jet of blood creates a wave which moves along the whole arterial system. The same phenomenon may be observed if water be injected by successive jerks into a narrow channel already full or nearly full, and open on the surface. Each fresh jet will create on the surface of the water in the channel a wave, which may be followed to its most distant extremity. This wave, even in a rigid tube, if sufficiently forcible, would communicate to the wall of the tube a thrill or vibration indicating the course which the wave takes. But in an elastic tube which yields under the injecting force the phenomenon is more distinctly perceived as the tube dilates under the pressure of the advancing wave.

It is important to notice that the phenomenon of the pulse in arteries is due solely to the wave excited by each successive injection

capillaries, with an almost even tenor of velocity, in the same manner as the spouting water of some fire-engines is contrived to flow with a more even velocity, notwithstanding the alternate *systoles* and *diastoles* of the rising and falling *embolus* or force; and this by the means of a large inverted globe, wherein the compressed air alternately dilating or contracting, in conformity to the workings to and fro of the embolus, and thereby impelling the water more equally than the *embolus* alone would do, pushes it out in a more nearly equal spout."—Hæmastaticks, p. 22, § 26.

of blood into the arterial system from the heart. The walls of the arteries have nothing to do with the causation of the pulse, but may render it more or less distinct according as they are more or less yielding.

The character or quality of the pulse will depend primarily and essentially upon the force of the heart,—secondly, upon the integrity of the mechanism by which that force is directed so as to drive the blood into the arteries,—thirdly, upon the quantity of blood in the vascular system,—and, fourthly, upon the condition of the arterial walls, according as it is apt to oppose or to yield before the wave caused by the heart's action. By reference to these points, we may explain the various conditions of the pulse observed in practice. Thus a weak heart, or a contracted arterial aperture, or a small supply of blood, will each equally produce a small pulse; while a certain power of heart, and an open unimpeded state of the arterial aperture, with a full supply of blood, are quite necessary to the formation of a large round pulse. But the qualities of softness or fulness, of hardness or wiryness, of compressibility, of incompressibility, all which are familiar to the *tactus expertus* of the practical man, are determined by the yielding or the resisting condition of the arterial wall.

Contractility of Arteries.—Arteries possess a power of contraction in virtue of the large quantity of elastic material which enters into the constitution of their wall; but this is a contraction which may occur in a dead as well as in a living artery, and which simply serves to restore to its medium dimensions an artery previously distended or stretched. They have, however, also a power of active contractility, which ceases with life, which is capable of being called into play not only by distension, but by other appropriate stimuli, and which can diminish the size of the vessels far beyond what their mere elasticity could effect, and even against the influence of the elastic force. This contractile power is due to the presence of unstriped muscular fibres in the arterial wall. The demonstration of these fibres in the walls of arteries by the microscope leaves no more doubt of the existence of a muscular contractile force in them than of its existence in the œsophagus or the intestine. Experiment anticipated anatomical research in pointing out that arteries contract as tubes do whose walls contain muscle, and it also indicated the peculiar manner in which the muscular fibres of arteries act. Under the influence of a stimulus even of so slight a nature as exposure to the air, an artery may be observed to contract very gradually, and to become very much diminished in size. Thus, in

one of Hunter's experiments, the posterior tibial artery of a dog was laid bare: it was observed, in a short time, to be so much contracted, "as almost to prevent the blood from passing through it, and when divided the blood only oozed out from the orifice." *

Mechanical stimulation, applied to a living artery, such as gentle friction with the point of a scalpel or needle, excites in its wall a slow and gradual contraction at the point stimulated, so that it appears constricted at that point. We have, by stimulating an artery in this way, at several points at some distance from each other, produced quite a moniliform appearance of it, causing a series of constrictions separated by portions in which the size of the artery was little altered. Verschuir was among the first to observe the effects of mechanical stimulation upon arteries, and he has recorded the results of his observations in his Inaugural Dissertation *de Arteriarum et Venarum vi irritabili*, published in 1766; and numerous experiments of a similar kind were performed in this country by our friend, Dr., now Sir Charles Hastings, which are detailed in his treatise on Inflammation of the Mucous Membrane of the Lungs, published in 1820.

The galvanic stimulus is also capable of producing contractions in arteries, but it requires to be repeatedly renewed before the effect is manifest. The most striking results from the application of this kind of stimulus, were obtained by the Webers, in their experiments with the rotatory magneto-electric instrument. The shocks were applied to the small mesenteric arteries of frogs, and a diminution of their diameter to one third was produced, in from four to ten seconds; and the contraction increased under the continuance of the stimulus, until the calibre of the vessel became from three to six times smaller than at first, so that only a single row of blood corpuscles could pass through it; at length the vessel became completely closed, and the circulation through it stopped.

From the combined evidence of anatomy and experiments, then, it can no longer be doubted that arteries possess an inherent contractility, in virtue of the presence of unstriped muscular fibres in their tunics. It remains to inquire, in what manner this power influences the circulation in the arterial system. Does it help to propel the blood? This question may be answered in the negative. The manner in which arterial trunks taper towards their distal extremities, renders it mechanically impossible that the contraction of circular muscular fibres around them would drive the blood onwards unless some valvular apparatus checked its passage back-

* Hunter on the Blood, &c. 4to. ed. p. 114.

wards or towards the heart. It is by reason of the existence of such an apparatus at the mouth of the aorta that the elastic coat of the arteries by its reaction propels the blood. But the muscular coat would not contract simultaneously at all points as the elastic coat does. It would, as in the œsophagus and intestines, act in successive portions—and the artery would, as in those tubes, be almost or altogether obliterated at the point of contraction. It is easy, however, to show that no such vermicular action takes place in the arteries, nor can it occur in tubes which, like them, are always and at all points filled.

It seems most probable that the contractile power of the arteries exercises a regulating influence upon the flow of blood through them. Its influence in this respect has long been recognized by practical men, under the name of *tone* or *tonic power*. It restrains within due bounds the distension of the arteries, limits the quantity of blood in each artery, adapts the size of the artery to the volume of its contents, and offers a certain amount of opposition or antagonism to the force of the heart.

It is owing to the resistance afforded by this contractile power of arteries to the passage of fluid into them, that the anatomist will fail to inject a tissue completely, if he attempt it too soon after death. The well known experiment of John Hunter, on the placenta, shows how long the contractile power will remain in the arteries of a part after its separation from the system, or after death. In a woman delivered on Thursday, the navel string was separated from the fœtus in the usual way, by tying the cord in two places, and dividing it between them—thus the blood was retained in the vessels of the cord and placenta. On the Friday morning, a ligature was placed an inch below the lowest of those ligatures, and that inch was cut off. The blood immediately gushed out, and, on watching the cut ends of the vessels, Hunter observed the arteries contracting with the whole of their elastic power, which took place immediately. The next morning (Saturday), on examining the mouths of these arteries, they were found quite closed up, so that in twenty-four hours the muscular coat had contracted to such a degree as to close up the area of the artery. On Saturday morning the experiment of Friday was repeated with another inch of the cord, with precisely the same results, but after its repetition on the Sunday, it was found on the Monday that the mouths of the arteries remained open, their muscular coat having by that time lost its contractility.*

* Hunter, *loc. cit.* p. 116. The muscular fibres of the arteries of a part recently

The difference in the results obtained by Hales, as regards the velocity with which certain fluids passed through the blood-vessels, is referrible to the contractile power of the arteries. Thus, while warm water, injected into the blood-vessels of a dog's bowels, passed in fifty-two seconds, the same quantity of common brandy took sixty-eight seconds; cold water (fourteen degrees above freezing) was eighty seconds longer in passing than the same quantity of warm water just before. A strong decoction of bark took much longer to pass through the vessels than the same quantity of warm water. Sixteen pots, of equally warm decoction of bark, were successively poured in, the first of which passed in seventy-two seconds; the sixteenth, " as the vessels grew more and more contracted by the styptic quality of the decoction," was 224 seconds in passing.*

This contractile power in the walls of arteries (their *tone* or *passive contraction*) is capable of modifying considerably the character of the pulse. When it is feeble, the artery offers but slight resistance to the entrance of the blood, and it therefore yields more completely under the force of the heart. Hence fulness of pulse and feebleness of muscular power or of *tone* in the wall of the artery, are apt to go together. On the other hand, an exalted muscular power or *tone* in the wall of the artery, by contracting the arterial tube, and resisting the flow of blood, would cause a *small*, *hard*, and even a *wiry* pulse; or a similar effect might be produced by an irritating fluid, as a diseased blood, passing through the artery. Again, failure of the tonic property of the arterial wall causes a *compressible* pulse; an excited or well-developed tonic power, will cause an *incompressible* pulse.

Of the Force of the Heart.—The blood encounters considerable obstacles to its passage through the vascular system, which tend to bring it to a state of rest. The friction against the inner surface of the vessels, and the resistance of the elastic and muscular elements of their walls to distension, must be overcome by any force capable of keeping up a continual renewal of the supply of blood to the several organs. Moreover, a certain rate of movement must be maintained in the blood's current. The attainment of these objects is clearly provided for, in the main, by the action of the heart, and that living pump is doubtless endowed with energies sufficient to drive into the blood-vessels renewed supplies of blood, with a

dead pass into the state of *rigor mortis*, like that of other muscles, which will last a certain time; the proper period for anatomical injections is either *before* the rigor mortis has come on, or *after* it has ceased.

* Hæmastaticks, p. 124, *et seqq.*

force and a velocity exactly adapted to overcome such natural obstacles as the action of the vascular system must naturally create.

To estimate the force of the heart, we must ascertain the pressure which the blood exercises on the walls of the blood-vessels during life, and we must measure the rate at which it flows through them.

A fluid flowing through a tube exerts a double force, one in the direction of the long axis of the tube, *the force of the stream*, of which the velocity gives a measure, and another, which is the pressure of the fluid against the wall of the containing tube or *the lateral pressure.* This latter force is always proportionate to the resistances which the fluid has to encounter to its flow. The longer the tube, through which the fluid passes, the rougher its walls, the narrower the opening through which it escapes, and the more glutinous the fluid, the greater the lateral pressure.*

A tube fixed into the walls of the tube through which the fluid flows, and at right angles to it, affords a simple means of measuring the lateral pressure, by the height to which the fluid will rise in it. By equally simple means we may measure both forces, if the measuring tube be prolonged into the other tube with its orifice opposite to the stream. The height which the column of fluid will attain in a tube so arranged, will indicate the altitude from which it must have fallen, to acquire the velocity and force with which it streams through the main tube.

Pitot, a distinguished French engineer, who lived about the middle of the last century, employed a tube of this kind for measuring the velocity of the stream in rivers. The tube was bent at a right angle, into two unequal branches, and the smaller or horizontal branch was immersed in the stream with its mouth opposed to it. The height of the column sustained in the tube afforded a measure of the force and velocity of the stream, that height being such as the water must have fallen from, in order to have acquired the same velocity.

Hales adopted a similar method to measure the pressure of the blood in the arteries. He inserted into the left crural artery of a mare, a brass pipe, whose bore was one-sixth of an inch in diameter; and to that, by means of another brass pipe, he fixed a glass tube of nearly the same diameter, which was nine feet in length. When the blood was allowed to flow into this tube it rose in it to a height eight feet three inches above the level of the left ventricle of the heart. After considerable loss of blood, however, the power of maintaining a column of this height ceased,

* See Volkmann, die Hæmodynamik nach Versuchen. Cap. i. Leipzig, 1850.

and the blood rose, after the successive bleedings, to seven, six, five, four, and at length to two feet four inches.

In a second experiment, exactly the same, excepting that it was made on a horse of more vigour than the subject of the previous one, the blood rose to nine feet eight inches, and fell subsequently, after successive bleedings, in the same manner as in the first experiment. A third experiment made upon a mare, consisted in fixing the brass pipe into the carotid artery towards the heart, and to that the windpipe of a goose, on account of its pliancy, and to the other end of that a glass tube, twelve feet nine inches long. The blood rose in the tube to nine feet six inches, and behaved, in all respects, much in the same way as in the former experiments. And afterwards, Hales experimented in the same way on the sheep, the deer, the dog, with results essentially similar, but varying with the size and general power of the animal.

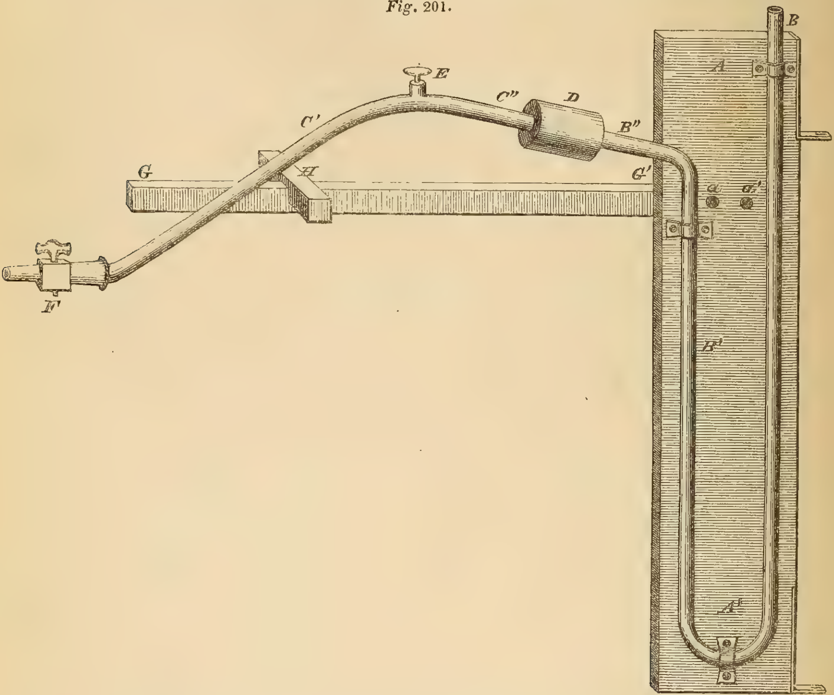
Hales estimated the force of the left ventricle of the heart at the moment of its systole, by multiplying the area of its inner surface into the height of the column of blood in the tube, which it was capable of sustaining, calculating also the absolute weight of the quantity of blood which formed that column. From these data he concluded that the contraction of the left ventricle of the horse's heart was capable of sustaining a weight of 113 lbs., that of the sheep 36·56 lbs., that of the dog 33·61 lbs., when the animal weighed 52 lbs., and 19·8 and 11·1 lbs. in dogs weighing respectively 24 lbs. and 18 lbs.

Poiseuille improved upon the method of Hales's experiments, and obviated some objections to them. He employed an instrument which he called *the hæmadynamometer*. (Fig. 201.) This consisted of a glass tube bent so as to form a horizontal (B″) and two perpendicular (BB′) portions. The horizontal portion is capable of being adapted by means of brass tubes of various size to arteries or veins, however different in calibre. The tube is attached to a board (AA′), on which a scale is marked. To use it mercury is poured into the perpendicular branches of the tube, and will, of course, stand at the same height in each when the instrument is kept in the perpendicular.

In order to prevent the coagulation of the blood, which by causing it to adhere to the sides of the tube would complicate the experiment (a point not provided against in Hales's experiments) a quantity of a strong solution of carbonate of soda is poured into the horizontal branch, and will therefore rest upon the column of mercury in the nearest vertical branch.

The instrument is now adapted by means of a pipe provided with a stopcock (F) to the artery in which the blood is to be measured. On opening the stopcock the blood rushes into the horizontal tube, mingles with the alkaline solution, and pushes down the mercury, in the vertical tube B′, that in the tube B rising to the same extent

Fig. 201.



Poiseuille's hæmadynamometer as slightly modified by Volkmann:—AA′ the board to which the bent glass tube (BB′B″) is attached. CC′C″ a tin tube which is fixed through a cork (D) air-tight to the horizontal branch of the glass tube. E an opening with a stopcock in this tube. F a conical tube which may be introduced into an artery or vein. This is provided with a stopcock which serves to regulate the admission of the blood into the tube of the hæmadynamometer. G H G′ an arm of wood connected with the board which serves to support the tin tube, and so protect the horizontal branch of the glass tube.

as the first is depressed. The rise and fall of the mercury in each vertical branch can be measured on scales placed behind them, and as the rise and fall are equal, the double of either will give the height of a column of mercury which the force of the stream of blood is able to maintain. By causing the blood to press upon a column of mercury, Poiseuille got rid of the necessity of having a very long tube as used by Hales.

Hales inferred, from his observations on the lower animals, and a comparison of the measurements of their arteries with those of man, that the force of the heart in the human subject is capable

of sustaining in a tube fixed in the carotid artery a column of blood $7\frac{1}{2}$ feet high, and calculating the surface of the left ventricle at 15 square inches, he concludes that when it first begins to contract the ventricle supports a pressure of 51·5 lbs. of blood. And Poiseuille assigns 4 lbs. 4 oz. as indicating the force which the left ventricle exerts at the moment of its contraction in propelling the blood into the aorta.

Volkmann combats the grounds upon which Poiseuille's calculation was formed; and assigns the heart's power as equivalent to the force which sets the stream of blood in motion, and gives it its proper velocity, and also to that which enables it to overcome the obstacles it has to encounter. This latter power is determined by the pressure in the artery, which is found in the mean, in the carotid artery of mammals, to be capable of supporting a column of mercury of 200 millimetres, or about 7 inches; or a column of blood of 2700 millimetres (mercury being 13·5 times heavier than blood); whilst the former force, taking the actual velocity of the blood in the commencement of the aorta at 400, and in the carotid at 300, would be represented by a column of blood a little more than 8 millimetres in height. Thus it would appear that the force of the heart may be expressed by the following formula—

$$H = 8{\cdot}2 + 2700 \text{ millim.}$$

or that it is capable of supporting a column of blood nearly 9 feet in height, which is equivalent to a column of mercury of about 8 inches.*

That the heart's force is extended to the whole arterial system and must therefore be highly instrumental in maintaining the circulation through it, is shown by the fact that a considerable pressure is exerted in the various arteries, which can be measured by the hæmadynamometer, or by other instruments. Poiseuille had affirmed, that the pressure in all the arteries was the same, a column of mercury of the same height being supported by the blood's pressure in all.† This doctrine, however, is at variance with every obvious

* See the remarks on this subject in the late Dr. Young's Croonian Lecture on the Functions of the Heart and Arteries. Phil. Trans. 1809, and republished in his Introduction to Med. Literature, 1823, p. 607 *et seqq.*

† As an example, the pressure in the carotid of a dog, distant 208 millim. from the heart, and that in the humeral artery 303 millim. distant, support a column of mercury of 179·04 millimetres. Whence Poiseuille infers that a particle of blood in the carotid, distant from the heart 208 millim., moves with the same force as a particle in the humeral artery, which has a distance of 303 millim.

hydrodynamic fact, as also with the results of other observations, of which those of Volkmann seem the most trustworthy. Volkmann shows that a fluid flowing through a system of tubes has to encounter at the point of its entrance into it the sum of the resistances which oppose it throughout the entire area, and these resistances determine the amount of pressure needed for its propulsion. Applying this to the arteries it is plain that in them the blood has to encounter the resistances in the capillaries, in the small arteries, in the middle-sized arteries, and in the arterial trunks, a fact, which by assigning to the resistance in each of these regions the symbols x, y, z, w, x representing that in the arterial trunks, and the other letters that in each of the remaining segments of the system, may be thus expressed, P (being the pressure in the commencement of the arterial tree) $= x + y + z + w$, whence it is plain that the amount of pressure cannot be the same in all parts of the arterial system, but diminishes steadily as the artery is more distant from the heart.

Spengler's experiments so far disprove the accuracy of Poiseuille's statement as to show that the pressure of the blood differs considerably in different arteries; but in the greater number of his observations the pressure appeared to be greater in the arteries more distant from the heart, some showing a difference of 36 millimetres in favour of the more distant artery; but in one of the instances quoted by Volkmann from Spengler there was a difference of 16·6 millimetres in favour of the carotid artery as compared with the maxillary.

But Volkmann's very numerous observations, made with more perfect instruments than those used by Spengler, show a marked difference of pressure in the near, and in the distant arteries. Thus, eight observations on the carotid, and a branch of the femoral artery of a large dog, gave a mean of 7·2 millimetres (0·27 inch) in favour of the carotid. And ten observations on the carotid and metatarsal arteries of a calf yielded a mean of 27 millimetres (1·05 inch) in favour of the carotid; and twelve observations on the same arteries of another calf gave a mean of 19·5 millimetres also in favour of the carotid. Volkmann has also shown, that in the same artery a notably greater pressure exists in the part near the heart than in that more remote from it, which is, of course, the more conspicuous, as the distance between the two points measured is greater.

Influence of Systole and Diastole.—Hales had observed, in his experiments with a simple glass tube, that a rise and fall took place

in the column of blood to a variable extent at and after each pulse. This observation has been confirmed by Ludwig, and also by Volkmann. The rise corresponds to the heart's systole, the fall to the diastole. This affords, in the greatest part of the arterial system, the clearest proof of the extension of the heart's influence throughout it. And Poiseuille showed that the pulsations of the heart could be counted by noticing the advance of the blood in pulses along the capillaries, and, under certain circumstances, even along the small veins.

Influence of Respiration.—That respiration exercises an influence upon the circulation has been likewise noticed by several observers. Hales had referred to this; he had noticed how the straining efforts of the animals which were made the subjects of his experiments, were followed by a rise of the column of blood in the tube, and how the same effect followed deep sighing. And Poiseuille found that during expiration the height of the column of mercury was much increased, but that it fell in inspiration. In forced and deep inspirations the force of the heart becomes so much diminished in some cases that no pulse, or at most a very feeble one, can be felt at the wrist: on the other hand, in forcible expirations the pressure of the blood in the arteries becomes double its normal amount. This has been further confirmed by Ludwig and Volkmann. The fact is of practical interest, and affords good reasons why the practitioner should caution those whose arteries are weakened by a diseased state of their tunics, against strong efforts, or against any action likely to disturb the quiet and freedom of the breathing.

The heart's force is materially weakened, as Blake's experiments show, by the introduction into the circulation of poisonous agents of a sedative nature. And there is every reason to believe that the existence of particular animal poisons in the blood, as the typhus poison, that of scarlet fever, of erysipelas, &c., is capable of depressing the heart and weakening the circulation.

Thus then, as far as regards the powers by which the blood is moved in the arteries, it may be stated that the circulation is maintained in them by the force of the heart; replaced and propagated throughout the system by the elastic reaction of the arterial tunics, and to a certain extent restrained or modified by the muscular contraction of the same tunic, which likewise serves very accurately to adapt the size of the arteries to the quantity of blood contained in them.

On the Velocity with which the Blood moves in the Arteries.—

The calculations of Hales and others on this subject, led to ideas respecting the velocity of the blood, which appear to be extravagant. Thus Hales inferred the velocity of the blood at the commencement of the aorta in man, to be at the rate of 735 feet in a second! The data upon which these calculations were founded are uncertain and unsatisfactory, such as the measurement of the area of the aorta at its origin, and the capacity of the ventricle and the quantity of blood expelled by each systole.

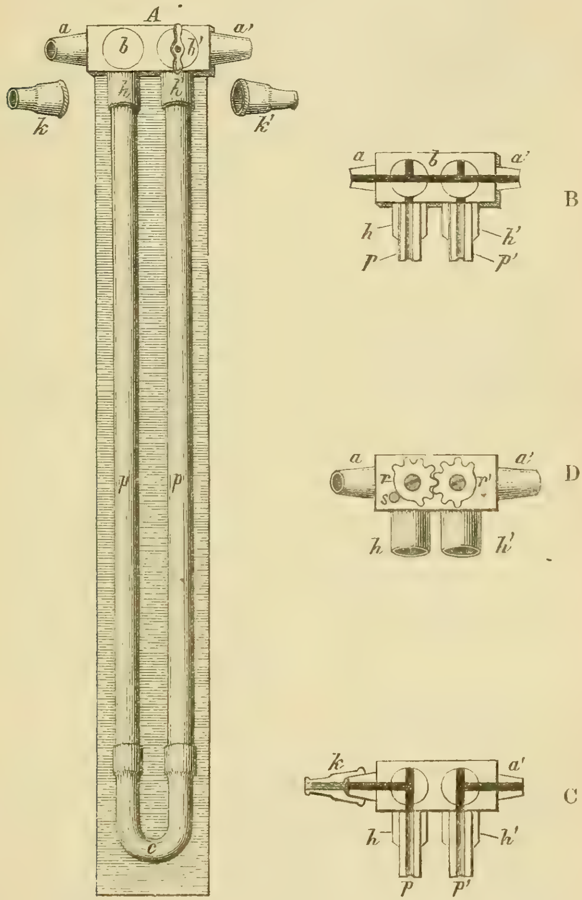
Volkmann has lately devised an instrument for the direct admeasurement of the rate of the blood's movement in the arteries. He calls it the *hæmodromometer.* It consists of a glass tube, containing water, 52 inches long, bent into the form of a hair-pin, which is substituted for a segment of the blood-vessel, in which it is required to measure the velocity of the blood's stream. The column of blood which comes from the heart pushes the column of water before it, without any great mixture of the two fluids taking place, and in passing through a determined space it takes a measurable time, whence it may be calculated how far the blood moves in a second.

The following description will explain the instrument and the mode of using it. At A (fig. 202) is a metal tube, an inch and a half in length; the ends of this (a, a') are conical, and fit into two corresponding conical tubes (k, k'), made like the pipes of an injecting syringe, so that they can be readily fitted into an artery. A stopcock (b') commands the channel of this tube, not only at a', but also, by two cogged wheels, at a. The mechanism of this arrangement may be readily understood, by reference to the adjoining sections of this portion of the instrument at B and C, and the view of its other surface at D (r, r' D). At h, h' are two short tubes, also of metal, which are fitted into the horizontal tube below the stopcock, and so that their channels (as shown at C) may communicate with, and be exactly equal to, that of the horizontal tube. The stopcock (b') commands this communication likewise. These short tubes (h, h') fit exactly upon the bent glass tube (p, p), and complete the communication between its channel, and that of the horizontal tube at its extremities. When the stopcock is turned so as to open the channel of the horizontal tube throughout, as at B, all communication with the glass tube is cut off: on the other hand, when the communication with the glass tube is opened, as at C, the channel of the horizontal tube is stopped, and fluid entering at a', would have to pass through h', and to traverse both limbs of the glass tube (p, p) emerging at a. For the protection of the

instrument in using it, the glass tube is attached to a board, to which is fixed a scale marked in metal.

In order, then, to use the instrument, a large artery is freely exposed for not less than three inches, and, after due precaution has been taken to counteract hemorrhage, it is divided by cutting out a piece; the conical pipes (k, k') are then fixed into the open ends

Fig. 202.



of the artery, one being directed towards the heart, the other towards the capillaries. They must be fixed far enough apart, to admit of the introduction of the horizontal tube (A) between them, without altering the usual direction of the arterial stream.

When this tube is fitted to the conical pipes, then the bent glass tube, previously filled with water, must be fixed to it by means of the short tubes (h, h', C), the stopcock being so turned as to shut off all communication with the glass tube. As soon as the instrument has been properly fixed in the artery, the blood is allowed to flow into the glass tube. It may be now seen to traverse the glass tube with a velocity very nearly the same as it has in the artery, and in doing so it pushes the water before it into the peripheral blood-vessels, with (according to Volkmann) only a very slight admixture between the two fluids.

By trials made with his hæmodromometer, Volkmann found, in the case of seven dogs, that the blood flowed in their carotids with a velocity ranging between 205 and 357 millimetres in a second; in that of horses, 306 to 234; in the metatarsal artery of the horse, 56, and in the maxillary artery of the same animal, 99; in the carotid of a calf, 431. The average velocity in the carotids of mammals is stated by Volkmann to be 300* millimetres in a second.

It results, likewise, from these observations, that the velocity of the blood in the large arteries, and also in the large veins, is considerably greater than in the capillaries; that the velocity in arteries is not uniform, but is suddenly increased at each systole of the heart; and that the blood moves most quickly in the arteries nearest the heart. It appears, also, that the blood's velocity is materially lessened by loss of blood, and that increased rate of pulse, which always follows considerable losses of blood, is no indication of a more rapid blood-current, but, on the contrary, often accompanies a retardation of it. The velocity of the blood-current is influenced not so much by the rate of action of the heart, as by the intensity of its systole, and the quantity of blood which it expels at each contraction.

Much was formerly said respecting the disposition of the arterial tree, being such that the combined areas of the branches of an artery exceeded that of the trunk, and that with each succeeding series of subdivisions, the blood flows into an increased area. Haller (tom. i. p. 77), ascribes the first observation of this kind to an Englishman named Cole.† It is repeated by Keill, Hales, and many others, among them John Hunter and Sir C. Bell. The general effect of such an arrangement would obviously be to diminish the

* Tolerably close approximations to the value of these measurements in English inches, may be obtained by dividing each number by 25.

† De Secretione animali. Oxon. 1674.

rate of movement of the blood as it flows from trunks to branches. But the careful measurements of Mr. Fernaby and of Mr. Paget, render it necessary to modify the general proposition to some extent.

Mr. Fernaby* compared the areas of trunks and branches in the only sound way, namely, according to the geometrical law, that the *areas* of circles are as the *squares* of their diameters. Estimated thus, he found that the excess of the combined areas of the branches over those of the trunks was very trifling, and, in some instances, scarcely appreciable; and Mr. Paget, while confirming the general statement of Mr. Fernaby, discovered a remarkable exception in the case of the common iliac arteries, whose combined areas were distinctly less than that of the aorta above the point of bifurcation—and the combined areas of the external and internal iliacs were less than that of the common—but those of the branches of the external iliac exceeded notably the area of their parent trunk.†

Volkmann states that in general the arterial capacity is increased in area by the division into branches. But he instances a remarkable exception in the case of the external and internal carotids of the horse, whose combined areas are smaller than that of the trunk. He remarks, likewise, that the first divisions of the larger arterial trunks (aorta and pulmonary artery) experienced very little increase of area; but that, as subdivision goes on, the increase becomes much more marked. And it is especially so near the capillaries, where the combined areas of some small branches nearly double that of their parent. This is particularly interesting, as denoting the coincidence of physical conformation with the result of direct observation, on the velocity of the blood, which shew that it is near the capillaries, that the most decided diminution takes place in the rate of the blood's motion.

Of the Circulation in the Capillaries.—The manner in which the blood flows through the capillaries is easily made the subject of direct observation by examining the transparent parts of certain animals, as the wings of bats, the mesenteries of small animals as the mouse, the web of the frog's foot, the lung of the frog, or of the newt, &c.

In watching the circulation in the web of the frog's foot under the microscope, with a magnifying power of about 200 diameters, the following points will attract observation: first, it will be seen that the stream is continuous, that is, it rushes with a considerable

* Lond. Med. Gaz. 1839.

† Lond. Med. Gaz. 1842.

velocity, which is uniform when not affected by any extraneous influence; the course and rate of the stream are indicated by blood-particles which are carried along in it, and which seem to chase each other through the various channels and among the little islands of the solid particles of the tissue which the blood is destined to nourish. These particles most frequently pass in a single row, with a variable interval between them: sometimes, however, they seem to rush in pairs, or in threes, according to the size of the capillary channels through which they flow. Secondly, it will be noticed that the greatest velocity of the stream is in its centre, a fact which comports with what is observed in rivers and other channels through which water flows, while towards the circumference the stream becomes much slower, so that the layer of fluid which is in immediate contact with the capillary wall is almost or completely still. The particles are carried along in the centre or rapid part of the stream, and but occasionally a solitary particle seems attracted towards the circumference. This is most frequently a colourless corpuscle, so that sometimes several colourless corpuscles are seen at intervals in contact with the wall of the capillary, as if drawn to it by some special attractive force, or moving much more slowly around the central mass of red particles. The sudden change from a rapid to a slow movement, or to perfect stillness, when one of these particles is thus drawn from the centre to the circumference of the stream, serves to display, in a very satisfactory manner, the peculiar feature of this portion of the contents of the capillary, which, from its apparent stillness and from the paucity of blood-particles in it, has been called the *still layer* of the *liquor sanguinis*. The existence of this still layer is doubtless a purely physical phenomenon, identical with that which is known to take place when fluids pass through inorganic capillary tubes, in which the circumferential layer seems to adhere or to be attracted to the wall of the tube, and it would clearly favour the transmission of nutrient or other material dissolved in the liquor sanguinis, through the wall of the vessel, in obedience to a force of attraction between the blood and the tissue. This still layer forms but a small portion of the whole capillary stream—perhaps about $\frac{1}{8}$th or $\frac{1}{10}$th its breadth; it is greater when the circulation is slower; it is also broader, and therefore more visible when a vessel makes a bend. The application of cold to the capillaries increases the breadth of this layer, whilst heat produces an opposite change.

The capillary vessels dilate or contract, under particular circumstances. Their dilatation is passive, and due either to an increased

pressure of the blood into them, or to their distension under the same pressure in consequence of diminished tone of their wall. Their contraction is caused either by an inherent contractile power in them, or by the diminution of their contents in consequence of the contraction of the capillary arteries, in which latter case diminished pressure permits them to contract, in virtue of the *elasticity* of their walls. This latter would be the more probable view, in default of any proved existence of a muscular structure in the walls of the true capillaries, but there is no good reason why the nuclei observed in them should not be regarded as belonging to muscular tissue here in a membranous rather than a fibrous form.

The rate at which the blood moves in the capillary circulation has been made the subject of direct observation by various physiologists. It is slower than in the smallest veins, and still more so than in the smallest arteries. Hales had stated the rate of the circulation in the capillaries of the muscles of a frog to be an inch in a minute and a half, and in the pulmonary capillaries five times that velocity. Subsequent observers, Weber, Valentin, and Volkmann, give a somewhat greater velocity: Weber and Valentin make it about an inch and three-quarters in a minute, and Volkmann found it about the same in cold-blooded animals, but twice as much in the capillaries of the mesentery of a young dog. These estimates are probably rather below the real rate of motion of the blood in the capillaries, if we allow for the degree of pressure and constraint to which they must be subjected in making the observations.

Of the Forces which maintain the Capillary Circulation.— The principal force by which the circulation is supported in the capillary system, is the *vis a tergo* of the heart. We have already adduced sufficient evidence to prove that that force is capable of driving the blood throughout the whole circulating system. The following facts may be stated in proof of this doctrine.

1. The pressure of the blood may be measured in the *veins*, in the same way as in the arteries, and this varies with the force of the heart. If, then, the heart's force extends to the veins, it must do so through the capillaries.

2. The capillary and venous circulation in any segment of the body, is greatly influenced by the circulation in the main artery of that segment. Thus, Magendie found the circulation much retarded in the femoral vein by stoppage of that in the corresponding artery: and by the hæmadynamometer it may be shown that the

force of the blood in the veins diminishes or increases with that in the corresponding artery under certain circumstances.

3. In Fishes, the whole blood ejected from the heart passes, from the bulbus aortæ, through the branchial capillaries, before it enters the systemic vessels; thus illustrating how the heart's force may be propagated through a complex network of minute capillaries, to both arteries and veins, as well as to the system of capillaries which intervenes between them.

4. In debilitated animals, it is evident, from the jerking movement of the blood in the capillaries, corresponding with the action of the heart, that the impulse of that organ is extended to these vessels, unbroken by the elastic reaction or the muscular contraction of the arteries. This may be well seen in watching the circulation in the frog's web, or in the tail of the tadpole.

Thus, there can be no doubt that the heart's force is not only fully adequate to, but is the principal agent in, the maintenance of the capillary circulation. When this force fails, the circulation in the capillaries suffers as much as, if not more than, that in any other portion of the vascular system; and the sluggish transmission of the blood through the capillaries, such as we often find when the heart is simply weakened, occasions congestions, particularly of dependent parts, and then, by the filtration of the serous portion of the blood through the parietes of the vessels, œdema and anasarca.

But however readily we may concede that the heart's action is the *principal* force, it must be confessed there are certain phenomena which do not admit of satisfactory explanation, on the supposition that it is the only one employed in the maintenance of the capillary circulation; and it seems more reasonable to assume the influence and exercise of some other force superadded to this, in order to explain various phenomena which take place in, or which are dependent on, the circulation through the capillaries.

The more remarkable of these phenomena are blushing, or, in more general terms, the influence of mental emotion upon the capillary circulation; the influence of local irritation, whether accidental or morbid; and the effects of asphyxia.

It seems highly probable that in the ordinary molecular changes which take place in the nutrition of the tissues, a force is generated, which, in its normal state, must promote, by an attractive influence, the flow of blood through the capillaries. The cessation of such a force would operate unfavourably to the flow of blood through the

capillary system, whilst its existence in greater power at one point than at another, would cause a greater afflux of blood in the former than in the latter direction.

The best illustration of the exercise of this force, which, for the sake of brevity, may be designated *the capillary force*,* is found in the circulation of the sap in plants. It is exercised in two situations—at the roots and in the leaves,—constituting in the one a *vis a tergo*, and in the other a *vis a fronte*. At the roots, a rapid imbibition of fluid takes place with such energy, that it pushes before it the fluid above; thus if the stem of a vine, in which the sap is rising, be cut across, a bladder tied over it, will, after a short time, be burst by the fluid accumulated beneath it; or if a bent tube, containing a column of mercury, be affixed to it, the mercury will be raised to the height of forty inches or more. And that a force of attraction is exercised at the leaves, may be shown by placing the lower end of the upper division of the cut vine in water, when an active absorption and circulation of water will take place as long as the vital changes in the leaves go on; but if the vine be taken into a dark room, so as to check these vital changes, the absorption and circulation will likewise cease. So also the elaborated sap or latex, which, from its containing the elements for the nutrition and for the various secretions of the plant, may be likened to the arterial blood of animals, circulates through a complex system of anastomosing vessels (like the capillaries of animals), in the under surface of the leaves and in the bark, and will ascend towards the stem, even against gravity, in a dependent branch. The circulation of these fluids takes place with the greatest activity in growing parts, in which nutrient and chemical changes are going on most actively.

Professor Draper, of New York,† has given a definite expression to the nature of the forces which operate in the production of the circulation of the sap in plants, and in that of the blood in animals. The laws of endosmose and exosmose resolve themselves into the following dogma:—"That if two liquids communicate with one another in a capillary tube, or in a porous or parenchymatous structure, and have for that tube or structure different chemical affinities, movement will ensue; that liquid, which has

* The name *Capillary* force, which was given by Dr. Carpenter, must be taken as merely denoting that the force is exerted *at* the Capillaries, whether it be exercised by their walls or by a mutual action between the blood within and the tissues outside them.

† On the Forces which produce the Organization of Plants. 1845.

the most energetic affinity, will move with the greatest velocity, and may even drive the other liquid entirely before it."

In plants, the rise of the ascending sap from the ground, results from the attractive force of the spongioles. These appropriate certain elements contained in the fluid, and exercise a more energetic attraction on a new supply, which pushes the former before it. Thus the sap ascends to the leaves, pushed on by successive new portions attracted to the spongioles. At the leaves, a new force of a similar kind, but due to the action of light, draws it on, and causes it to push before it the newly formed latex or elaborated sap, the flow of which is promoted by its affinity for the vegetable tissues which it permeates.

In the systemic circulation of animals, the arterial blood has a great affinity for the tissues to which it is brought by the capillary system. This force of attraction draws on the blood from the arterial side of that system, with a power which helps to propel on the de-oxygenized blood into the venous radicles. In the pulmonary circulation, venous blood is conveyed to the air-cells by the pulmonary arteries. This kind of blood has a great affinity for the oxygen which is being continually brought to those cells by the movements of respiration. It is therefore forcibly attracted to the air-cells, and, being charged with oxygen, is pushed on by the succeeding portions of venous blood, which the same force is constantly attracting.

It is by the influence of an attractive force, such as Professor Draper describes, that we can best explain the continuance of a complex circulation in many of the lower animals in which no central organ of impulsion exists, as in some of the Polypifera, and of the Articulata. In the sponge the remarkable currents of water which flow through the various channels that penetrate its substance, are maintained without any special propelling organ whatever. And the beautiful *cyclosis* in Chara and Valisneria affords a striking instance of a circulation without *vis a tergo.*

In the vascular area of the egg a circulation exists before a propelling organ. And in the acardiac fœtus a similar circulation exists, although in general it has such a connexion with a second perfect fœtus that the heart of the latter may influence the circulation of the former. But that a fœtus may grow to a considerable size, and have its various tissues well developed without any connexion with the twin fœtus, by means exclusively of a circulation of its own, of which a heart forms no portion, or upon which it can exercise but a very remote influence, is shown by the case

put on record by the late Dr. Houston.* No doubt the same law which influences the movement of fluids in vegetable tissues would be in operation in such cases.

Now with reference to the phenomena in the circulation of the blood in man above referred to, it may be asked is the assumption of the exercise of a capillary force necessary for explaining them? Can blushing, and other local determinations of blood be accounted for, if we admit a *vis a tergo* as the sole force of the circulation? In order to explain the accumulation of blood, in the cheeks for instance, under the influence of mental emotion, the advocates of the latter doctrine suppose the capillaries muscular, and affirm that a relaxed state of the walls of the capillary arteries, and perhaps also of the capillaries themselves, is produced by the nervous change which mental emotion excites. Such an explanation is perfectly admissible in this particular case, and it seems highly probable that in the relaxed state of the capillary vessels of the face, their walls yield under the pressure of the heart more than those of neighbouring vessels which do not come so completely within the range of the centre of emotion. And in many persons, emotion causes the blood to desert the cheeks, which in consequence become pale. In such cases the change in the nervous centre must excite an opposite, that is, a contracted state of the capillaries of the cheeks.

But the accumulations of blood which are caused by local irritations, do not admit of satisfactory explanation by mere changes in the capillaries of the affected part.

For example, a particle of dust is thrown into the eye, and as long as it is in contact with the conjunctiva, its capillary vessels are turgid with blood. Is this due to a relaxed state of the capillaries caused by the presence of an irritating agent? The analogy of the influence of mechanical stimulation upon other vessels would lead us to infer that the irritation of a particle of dust in contact with the conjunctiva would cause the capillary vessels to *contract*, and a contracted state of these vessels would oppose rather than favour the accumulation of blood in them. It seems much more reasonable to suppose that the irritation caused by the foreign particle, increases the attractive force which the tissue naturally exercises on the blood; and this would give us a clue to explain the two kinds of congestion long recognised by practical men, the *passive* and the *active* form. The former is owing simply to a relaxed flaccid state of the parietes of the blood-vessels

* Dublin Medical Journal, vol. viii.

which permits them to *receive* a greater quantity of blood from the heart, and to a *minus* state of the capillary force, the other to a *plus* condition of that force,—in virtue of which the tissue *attracts* a greater quantity of blood. To this latter form of congestion pathologists give the name of inflammation. Its phenomena, as observed under the microscope, are such as a *vis a tergo* alone could not develope. For not only are there dilatations of the vessels of the inflamed part, and a great afflux of blood towards a certain point or points in it, but the blood-corpuscles seem to rush thither, as if forcibly attracted towards each other, and also to some common focus. And the rapid and copious process of exudation, and the formation of pus-cells, which are so apt to follow an attack of inflammation, afford further strong indication of augmented vital force in the inflamed part.*

So also in growing tissues, and in organs which enlarge at particular times, or under certain circumstances, the increased flow of blood to the part is a phenomenon in close analogy with the increased flow of sap to a bud; and is due not to a *vis a tergo*, or to a relaxed state of blood-vessels, but to a demand from the tissue for more blood, an attractive force, by which the direction is regulated, and the quantity also. The annual renewal of the antlers of the stag, the enlargement of the testes of birds at particular seasons, that of the breasts of women during pregnancy and after parturition, all these cases afford instances in which a demand for blood is created at some point of the periphery, and a greater flow is established to the organs there placed than previously took place to them.

We can afford no satisfactory explanation of the localization of certain changes in the capillary circulation, unless on the hypothesis that the constituent elements of the affected parts are primarily diseased, and that their demand for blood is, in consequence, increased or diminished, and the flow of blood regulated accordingly. Thus the developement of gout in a joint takes place often with such rapidity that it appears to the patient to be sudden; the train of phenomena being in such cases, first, a change in the tissues, so gradual as to be unperceived, then, an increased flow of blood to such an extent as to cause the heat, the throbbing, and pain which characterize such affections. Again, certain poisons, which seem as it were to spend their force, in great part at least, on the skin, do not cause a change in the whole capillary circulation so much as

* The theory of inflammation is extremely well discussed in Mr. J. Simon's Lectures on Pathology, Lect. IV. See also Mr. Paget's Lectures on Inflammation.

in points of it, here and there, determining an increased flow of blood to this point and that, and leaving the intervening parts unaffected. The well-ascertained fact, *ubi stimulus, ibi fluxus*, cannot be so well explained on the hypothesis that the stimulus creates a relaxation of the tunics of the capillaries of the part, because that is opposed to analogy, as on the supposition that under the operation of the stimulus the demand for blood in the tissues is augmented, and the capillary force becomes exalted in the part, in virtue of which a greater flow of blood is determined to it.

The phenomena of asphyxia show that a stoppage of the circulation may take place at the capillaries, notwithstanding the continuance of the heart's action. When the access of air to the lungs is excluded, the circulation ceases at the pulmonary capillaries, and on examination after death the left auricle and ventricle are found quite empty, and the right cavities of the heart gorged with blood. The repletion of the latter cavities, and the emptiness of the former, indicate the position at which the obstruction to the circulation took place. Instantly the air is re-admitted to the lungs, the blood assumes a bright red colour and the circulation goes on, indicating that the changes which take place between the air and the blood, must generate a force which exercises an important influence on the capillary circulation, and without which the heart's force is insufficient to propel the blood through the pulmonary vessels. Dr. John Reid* argues, as we think with justice, from the instantaneousness of the restoration of the circulation on the re-admission of air, that its stoppage must be due to the cessation of the respiratory changes, and not to a contracted state of the capillary arteries as suggested by Mr. Erichsen, because the relaxation of those arteries, like their contraction, is a slow process, requiring two or three minutes to accomplish it.†

* John Reid, on the Cessation of the Vital Changes in Asphyxia. Phys. Researches, Edinb. 1848.

† Our friend and colleague, Dr. Geo. Johnson, has discovered a very interesting point, connected with the minute vessels of the kidney in cases of chronic nephritis with shrinking of the organ, which furnishes an additional instance of retardation or stoppage of the circulation at the capillaries, despite the continuance of the heart's action. Dr. Johnson shews that under the influence of defective secretion, the renal circulation is greatly retarded in the *intertubular* capillaries, and that the *Malpighian* capillaries are consequently subjected to a greatly increased pressure and distension, giving rise to an escape of serum, or of blood when a rupture of one or more of the minute vessels has occurred. When such a state of vessels has been of long duration, as in chronic inflammation of the kidneys, Dr. Johnson finds the capillary arteries much thickened, by reason of hypertrophy of their circular and longitudinal

On the whole we are disposed to the following conclusion respecting the capillary circulation, namely, that it is maintained by the *vis a tergo* of the heart; but it is regulated and modified partly by the elasticity of the walls of the capillary blood-vessels, partly also by their contractility, which is greatly influenced by changes in the nervous system, but chiefly by the operation of a force, developed by those chemical and physical changes, which take place between the blood and the tissues, and in which the phenomena of nutrition essentially consist. For the due exercise of this force a normal constitution of both the blood and the tissues is the most important condition.

Of the Circulation in the Veins.—The blood moves in the veins in a continuous stream, a fact sufficiently apparent to all who have watched its escape from a vein after venesection, and as is likewise apparent in examining the circulation in minute veins under the microscope. The velocity of the venous current is considerably less than that of the arterial, but greater than that of the capillaries, and, as Volkmann has shown, it increases in the veins which are nearest to the heart.

That the *vis a tergo* of the heart is sufficient to maintain the circulation in the veins is abundantly proved by all those facts which have been already recited with reference to its influence on the capillary circulation. Of these the most important are the experiments of Magendie, already referred to (p. 369), and the fact that in states of debility a distinct venous pulse is formed synchronous with the heart, and evidently resulting from the extension of the heart's impulse through the capillaries. Such a pulse (which may be called the systolic venous pulse) is in rare instances observable in the human subject in states of great prostration of strength,

fibres, and a thickened and opaque state of the walls of the Malpighian capillaries; while the intertubular capillaries and veins remain unaltered, save in a diminution of their number, some having become wasted and obliterated in consequence of the arrested action of the secreting cells. These observations show an obvious connexion between the activity of the organic changes connected with the act of secretion and that of the capillary circulation, and, indeed, an interdependence between the movement of the blood and the secretory function of the gland; but the hypertrophy of the muscular fibres of the capillary arteries seems rather to indicate that in these extreme capillary arteries, some propulsive power (*vis a tergo*) may be exercised by their muscular fibres in promoting the flow through the capillary system.—See Dr. Johnson's Paper on Albuminous Urine and Dropsy in the 33rd vol. of the Med. Chir. Trans.

but has been most frequently noticed in observations on the circulation of cold-blooded animals.

Pulsations synchronous with the heart's beats may be not uncommonly noticed in the human subject, which it is important that the observer should not confound with those resulting from the extension of the heart's impulse, as above referred to. These may be called the *regurgitant*, and the *communicated* venous pulse. The former is caused by the regurgitation which takes place from the right auricle into the large venous trunks connected with it at every systole of that cavity. In a state of health, the regurgitation is so small that its influence extends only to the larger veins—but when the right cavities of the heart are dilated, a much larger quantity of blood is regurgitated and a distinct venous pulse is visible in the superficial jugular veins, and sometimes in all the superficial veins which are distributed over the neck and upper part of the chest. The communicated venous pulse results simply from the proximity of some large artery which in its pulsations communicates to the vein a movement of a similar nature.

Hales and Poiseuille estimated the force of the current of blood in the veins; the former by the introduction of tubes into the large veins, as in his experiments upon arteries, the latter by the hæmadynamometer, and their observations have lately been repeated by Valentin and Mogk. Hales found that the blood rose to four feet two inches above the level of the heart, in a tube inserted towards the head into the jugular vein of a mare, the blood rising several inches when the animal strained, but subsiding again when he became quiet; hence it is plain that the force of the heart, competent as it is to maintain a column of such a height, must be amply sufficient to return the blood to the heart. Valentin and Mogk's observations show that the force of the blood in the veins of dogs is equal to one-eleventh or one-twelfth of that in the corresponding arteries.

The venous circulation is influenced a good deal by the respiratory movements, which tend partly to promote, partly to retard it. These effects are produced most plainly by the forced movements of respiration. Thus a deep inspiration, by enlarging the capacity of the chest, generates a tendency to a vacuum which, under the pressure of the surrounding atmosphere, is filled chiefly by the rush of air into the trachea, and through it to the lungs, but partly by the afflux of the blood, which must be principally venous, since the semilunar valves would oppose any reflux in both the great arteries. Sir

David Barry illustrated the influence of inspiration in favouring the centripetal flow of blood. He introduced one end of a bent glass tube into the jugular vein of a horse, the vein being tied above the point at which the tube was inserted: the other end of the tube was immersed in a coloured fluid. At each inspiration the fluid rose in the tube, being drawn towards the chest, whilst during expiration it sank or remained stationary.

Forced expiratory efforts, on the other hand, retard the venous circulation, as may be well illustrated by holding the breath for a few seconds, or straining strongly, when the veins, especially those of the neck and chest, will swell up and become distended; but as soon as the breathing is restored, they return immediately to their former size. Hence it is that persons subject to frequent disturbances of the respiratory actions, as in asthma or dyspnœa of any kind, exhibit, after a time, more or less enlargement of the venous system.

Disturbances in the respiratory actions seem to affect the circulation and especially that in the veins, more extensively in another way, namely, through the pulmonary capillaries. The imperfect respiratory changes, consequent upon the disturbed breathing, retard the flow of blood through the capillary plexus, which undergoes, by the dilatation and rupture of the air-cells, considerable stretching and widening of its meshes, and even becomes obliterated in parts. These changes also create additional obstacles to the pulmonary circulation, which impede the flow from the right ventricle, and increase the backward pressure of the blood on the walls of that cavity, causing it to become dilated and hypertrophied. It is, in this way, that are produced the hypertrophy and dilatation of the right cavities of the heart, which, to a greater or less extent, are invariable consequents of frequent attacks of asthma or bronchitis.

The influence of the respiratory movements upon the venous circulation is shown in the clearest manner by the use of the hæmadynamometer, as in the experiments of Poiseuille, Magendie, Ludwig, Valentin, and Mogk, the column of mercury rising in expiration, and falling in inspiration; and these experiments likewise prove that this influence is only felt in the large veins near the chest, and not in the more distant ones. The influence of expiration in retarding is much more powerful than that of inspiration in promoting the venous circulation, for the same physical condition of the chest which exists at the commencement of inspiration, and which favours the rush of blood to it, tends rather to delay the

escape of blood through the arteries, and the heart's action is thereby much weakened and often depressed.

Muscular movements likewise favour the venous circulation, as is well shown in the operation of venesection, when the patient is made to move his fingers freely, the flow of blood from the vein being thereby immediately increased. It is the action of the valves which determines the centripetal flow of the blood in the veins under muscular pressure, for as the contracting muscles simply compress the veins, the blood would be driven either or both ways; but the valves affording a direct impediment to the centrifugal flow, it is forced to take the opposite course. This is obviously one of the ways in which exercise favours the circulation and promotes the general health.

It has been supposed that the contraction of the auricles by partially emptying those cavities, calls into play an elastic force in their walls, which favours the rush of blood into them, and that thus a certain suction power of the auricle may be enumerated among the forces which aid the venous circulation. The idea is illustrated by exhausting an India-rubber bag, to which a glass tube is attached, and then immersing the open extremity of the latter, in a vessel of water, when the water will pass freely into it under the influence of the atmospheric pressure on the water. The principal fact in favour of this view is the experiment of Wedemeyer, which is thus detailed by Müller. "Wedemeyer and Guenther having tied the jugular vein of a horse, made an opening into it between the ligature and the heart, and introduced a catheter, to which a bent glass tube had been cemented. The longer descending branch of the tube (two feet in length) was placed in a glass filled with water. At first the inspirations and the contractions of the heart were nearly simultaneous, and of the same frequency,—namely, thirty in a minute,—and the coloured water rose suddenly two or more inches in the tube at the moment of each inspiration and pulsation of the heart, and sank again each time to its former level. The inspirations gradually became twice as frequent as the pulsations of the heart, and Wedemeyer and Guenther now observed, for a long period, that the rise of fluid did not take place at each inspiration, but at every beat of the heart, and, consequently, simultaneously with each dilatation of the auricle. This experiment," adds Müller, "seems to prove beyond doubt that the heart exerts a power of suction." It is most probable, however, that this power is extremely small, and that it does no more than counteract the obstructive influence which would otherwise arise

from the regurgitation which takes place, into the large venous trunks from the auricles at each systole.

The veins possess a certain tonic influence similar to that of arteries, by which they can adapt themselves to the varying quantity of their contained blood. This is doubtless due to the presence of muscular fibres in the tunics of veins already described; the power of these fibres to alter the calibre of the vein is clearly demonstrable by the influence of galvanism,* which causes an appreciable diminution in the size of the vessel at the point of transit of the current.†

The flow of blood in the veins, then, it may be concluded, is maintained chiefly by that same force through which it is driven through the arteries and capillaries, aided by the sort of suction in the centripetal direction which is caused by inspiration and by the diastole of the auricles, and promoted likewise by the contraction of the various muscles, among or through which the veins pass, and by the position and mechanism of the valves.

It is proper to observe that the venous circulation being moved by less force than the arterial (the heart's power having already very much expended itself on the arteries and capillaries), is more influenced by gravity—either favourably or otherwise—than the arterial. Hence, in dependent positions, as in the lower extremities, when the blood has to ascend against gravity, the veins are apt to swell, and to acquire a permanent dilatation and thickening of their coats from the retardation of the current

* See Kölliker's experiments—Subold and Kölliker's Journal.

† While these pages were passing through the press (Feb. 1852), Mr. Wharton Jones announced, in a paper read to the Royal Society, the discovery that the veins of the bat's wings contract and dilate *rhythmically*, and that they are provided with valves, some of which completely, others only partially, oppose regurgitation of blood. The rhythmical contractions and dilatations are constantly going on, and that at the rate of ten contractions in the minute. During contraction the flow of blood in the vein is accelerated, and on the cessation of the contraction the flow is checked, with a tendency to regurgitation. But this check is usually only momentary; already, even while the vein is in the act of again becoming dilated, the onward flow recommences and goes on, though with comparative slowness, until the vein contracts again. It is the heart's action which maintains the onward flow of blood during the dilatation of the vein, whilst it is the contraction of the vein coming in aid of the heart's action, which causes the acceleration. Mr. Jones states that he has not been able to observe unequivocal evidence of tonic contractility in veins, as Kölliker's experiments indicate; he, likewise, affirms, in opposition to a statement of Mr. Paget, quoted at p. 330, that nowhere do the arteries and veins of the bat's wing communicate, the only communication being the usual one through the medium of capillaries.—Proceedings of the Royal Society, Feb. 1852.

in them. It is important that this fact should be kept in view by the practitioner in the treatment of varicose veins, and of anasarcous states of the limbs.

We have seen that the blood moves in the arteries with considerable velocity, and likewise with great, although much diminished, rapidity in the capillaries; its rate of motion increasing again in the veins, especially in those nearest the heart. It may be inferred from these facts, that any given particle may complete the round of the circulation in an exceedingly brief period. It is an important problem—especially with reference to the time in which poisonous substances introduced into the blood may produce their effect—to determine in what space of time a substance introduced into one part of the circulation may reach the most distant part; or how soon, for instance, a substance inserted into the *right* jugular vein may, after traversing the right heart, the pulmonary circulation, the left heart, the systemic arteries, return to the systemic veins, and be found in the *left* jugular vein.

In the present state of our knowledge no exact solution of this problem can be given. But a very close approximation to the truth may be obtained,—first by calculation, secondly by experiment. By calculation we can determine in what space of time the whole blood of the body may circulate through the heart. The data for this problem are, the weight of the whole quantity of blood in the body, the quantity of blood expelled at each systole from the left ventricle, and the number of systolic actions in a minute, or, more exactly, the duration of a pulse. It is plain that if the left ventricle contract seventy times in a minute, and at each contraction expel five ounces of blood, according to Valentin, or six ounces ($\frac{1}{400}$th part of the weight of the body), according to Volkmann, a quantity of blood equal to that of the whole body will in that space of time pass through the heart. It may, then, be assumed from calculation, that the circulation may be completed in a period of time, which, in round numbers, may be expressed as one minute.*

* Volkmann's formula is $t = z\,\frac{x}{y}$ where t is the required mean time of the completion of the circulation, x is the whole quantity of the blood, y the quantity expelled at each systole, and z the mean duration of a pulse. Whence, taking the mean quantity of x at 30 lbs., and of y at 6·2 ounces, the duration of a pulse being 0·85 of a second, we get $t = 0{\cdot}85\,\frac{15000}{188} = 67{\cdot}5$ seconds. And as, according to Valentin, the whole quantity of blood is equal to about 1-5th the

Hering was the first to experiment on this subject, his object being to ascertain how soon a substance easily recognized (as ferrocyanide of potassium), when introduced into one part of the circulation, as the right jugular vein, could be detected in a distant part of the circulation as the left jugular. Hering found that this substance would pass from the right to the left jugular veins in from twenty to thirty seconds; and from the jugular vein to the great saphena in twenty seconds; from the jugular vein to the masseteric artery in from fifteen to thirty seconds. Results quite confirmatory have been obtained from like experiments by Poiseuille, and also by Blake. The former found that ferrocyanide of potassium, with acetate of ammonia, or nitrate of potash, passed from one jugular vein to the other, in from eighteen to twenty-four seconds; but that the addition of alcohol retarded the rate of transit to from forty to forty-five seconds. Blake found that nitrate of baryta passed from the jugular vein of a horse to the opposite carotid artery in from fifteen to twenty seconds. He found also that the poisonous influence of strychnia on the nervous system, showed itself in twelve seconds after injection into the jugular vein; in a fowl, in six seconds and a half; and in a rabbit in four seconds and a half.*

The results obtained from calculation as regards the rate of the circulation, are less conclusive than those by experiments, for the obvious reason that we have only the approximative value of the two principal quantities which enter into the calculation, namely, that of the mass of blood in the body, and that expelled at each systole. But the results of the two modes of inquiry are sufficiently near to each other, to denote that the round of the circulation is completed by any given portion of blood in a marvellously brief period, which, in man, probably, rather falls below than exceeds a minute. We need not, therefore, have recourse to any other hypothesis to explain the rapid effects of certain poisons, than

weight of the body, and as from Volkmann's researches the quantity expelled at each systole of the ventricle is $\frac{1}{400}$th of the weight of the body, calling this weight p, then $x = \frac{1}{5} p$ and $y = \frac{1}{400} p$, and $t = z \frac{80\,p}{p}$ therefore $t = 80\,z$, whence it appears that the time of the circulation is directly as the duration of a pulse, and inversely as its frequency.

* Hering in Tiedemann and Treviranus Zeitschrift fur Physiol. b. iii. Poiseuille's Ann. des Sc. Nat. 1843. Blake Edin. Med. and Surg. Journal, 1841. See also on this subject Volkmann's 10th chapter.

that they enter the blood, and with it are whirled with immense velocity through the substance of the most vital organs.*

* On the subjects discussed in the preceding chapter, the reader is referred to the various systematic works on Physiology, to the supplement lately published by Valentin, and to Dr. Allen Thompson's very comprehensive article 'Circulation' in the Cyclopædia of Anatomy and Physiology. On the anatomy and physiology of the heart, Kurschner's article in Wagner's Handworterbuch, and Dr. Jno. Reid's article in the Cyclop. of Anat. may be consulted; and as regards its motions and sounds, we refer to the reports of the Committee of the British Association collected in the Appendix of Dr. C. J. Williams's work on Diseases of the Lungs, to Dr. Blakiston's admirable work on Diseases of the Chest, to Dr. Walshe on Diseases of the Heart and Lungs, and Dr. Herbert Davies on the same subject; and on the physics of the circulation to Hales's Statical Essays, vol. ii.; to Dr. Young's Croonian Lecture on the Functions of the Heart and Arteries, Phil. Trans. 1809, and Medical Literature, p. 605; Poiseuille sur la Force du Cœur Aortique in Magendie's Journal, vol. viii., and his essay, Recherches sur l'Ecoulement des liquides considéré dans les Capillaires Vivans, in the Jour. des Sc. Nat. 1843; to the Essays of Ludwig, Spengler, and Mogk, in Müller's Archiv.; Magendie, Leçons sur les Phénomènes Physiques de la vie, and especially to the very able work of Volkmann, Die Hæmodynamik nach Versuchen, Leipzig, 1850, which we only received when these pages were in type. The following works may also be mentioned as containing interesting matter relating to the circulation in general,—Dr. Graves's Clinical Lectures, lect. i. on the Circulation; Dr. Todd's three Clinical Lectures on the Pulse, Lond. Med. Gaz. 1851; Draper on the Forces which produce the Organization of Plants, New York, 1845; Prof. Jno. Reid's essay on Asphyxia in his Physiological and Pathological Researches, ed. 1848.

CHAPTER XXIX.

ON RESPIRATION.—COMPARATIVE ANATOMY OF THE RESPIRATORY ORGANS. —ANATOMY OF THE HUMAN LUNGS.—TRACHEA.—BRONCHI.—BRONCHIA.—ULTIMATE PULMONARY TISSUE.—MOVEMENTS OF RESPIRATION. —FREQUENCY OF RESPIRATIONS, AND RATIO TO THE PULSE.—AERIAL CAPACITY OF THE LUNGS, AND AMOUNT OF AIR BREATHED.—CHANGES IN THE RESPIRED AIR, CARBONIC ACID EXHALED—OXYGEN INHALED. —CHANGES IN THE BLOOD.—NATURE OF THE RESPIRATORY PROCESS.

Respiration is that function by which an interchange of gases takes place between the interior of an organized being and the external medium; and in the animal kingdom oxygen is the gas received, and carbonic acid the gas given out. Every part of the surface to which the outer medium (whether air or water) has access may be considered to share in respiration, but in all, except some of the lowest animals, special organs are provided in which the interchange can be more readily effected. These organs in all cases consist of a membranous surface, adapted for contact with the surrounding medium and capable of exposing the fluids of the body in an especial manner to the action of the air. The interchange of the gases through this *respiratory membrane* is essentially a purely *physico-chemical* phenomenon, and must be studied as such. The very great variety of structures with which different animals are furnished for this function merely present us with modifications of the elementary conditions, whereby its activity and extent are governed in the several instances. The contact of air with the blood may be influenced (1) by atmospheric concentration or dilution. In water-breathing animals, the air breathed is that held in solution in the water, and is of course in very small quantity. The density or rarity of the air, according to temperature and barometric pressure, may perhaps affect the activity of respiration in air-breathers. (2) The extent of the respiratory surface, (3) the thickness of the tissue between the air and the blood, and (4) the more or less complete manner in which the general mass of the blood is brought from the tissues to the respiratory surface,—all these exert much influence on the activity of respiration.

Comparative Anatomy.—In *Entozoa, polyps, and medusæ,* no special respiratory organ exists. In star-fishes, and sea-urchins, among the *echinodermata,* the sea water gains access to cavities among the viscera, and is renewed continually by special organs, principally cilia. The holothuria has an internal system of arborescent tubes opening from the cloaca, receiving water, and, according to Tiedemann, serving for respiration; its branches end in vesicles. In *annelida* there are sometimes tufted *branchiæ,* or gills, as in the arenicola, or sand-worm, sometimes sacs opening separately, as in lumbrici and leeches. The *crustacea* have branchiæ attached either to the feet or abdominal surface. Of the *arachnida,* some, as the scorpion, have pulmonary sacs, or *lungs,* with parallel lamellæ, situated on the abdomen in from one to four pairs, and each opening by a separate stigma; others have a system of ramified internal air-tubes, termed *tracheæ,* or *spiral vessels* (from a spiral thread in their wall); and some both tracheæ and pulmonary sacs. The *myriapoda* and all the *insecta* have tracheæ. These penetrate the internal organs to their remotest parts, anastomosing freely, and open at several points on the surface. Insects which breathe in water, as well as many aquatic larvæ, have branchiæ which first separate air from the water, and then transmit it along the tracheæ. The respiration by tracheæ is probably a very perfect one, the blood and tissues being aerated throughout the body, at every spot in which they are being deteriorated.

Among *Mollusca,* some have *branchiæ,* or gills, as the cephalopods, the conchifera, and some gasteropods. Other gasteropods have a pulmonary sac, or *lung, e.g.,* the common snail. This sac opens and shuts so as to change the air, and on its surface the venous blood is distributed ere it reaches the heart.

Fishes present the greatest development of *gills.* There are four branchial arches, bearing vascular plates with lateral offsets. Matteucci estimates the surface of the gills of the common ray to measure 2250 square inches. All the blood is driven by the heart through the gills, to the aorta, and thus comes into close proximity to the water, in contact with the branchial surface. The capillary network has close and regular meshes.

Reptiles have a rudimentary form of lung, combined in many instances with gills, during a part or the whole of life, *e.g.,* in the frog the gills exist only in the tadpole state: in the proteus they remain through life. The pulmonary sacs of reptiles are more or less cellulated on their inner surface, and receive a portion only of the venous blood in each circuit.

In *Birds* and *Mammalia* respiration is much more active, being performed by means of large and highly divided lungs, placed within a bony framework, capable of receiving and rapidly renewing the air in large quantities, and giving passage to the whole blood of the body on its way from the veins to the arteries. In Birds there is a series of openings from the pulmonary air-tubes, by which the air gains access to passages and spaces among the other organs and tissues, rendering the body specifically lighter, and, perhaps, in some degree, aiding respiration. Further varieties in the structure of the lungs, modifying their respiratory power, will be alluded to when the human lungs have been described.

Organs of Respiration in Man.—The *lungs,* placed in the thoracic cavity, receive *air* by the nasal passages and trachea, and *venous blood* from the right side of the heart to transmit it to the left.

They form a double organ, with a single common air-tube, the *trachea*, and a single common *pulmonary artery*, supplying the venous blood. These vessels branch first into a right and left, and then into many subordinate ramifications up to the ultimate air-cells and capillaries. Four veins carry off the aerated blood to the left side of the heart. Being penetrated by the air, the lungs are the lightest organs in the body. In the fœtus, before breathing, they are small, and transmit only so much blood as is requisite for their own growth, but when the air enters, their volume augments, their absolute weight increases in consequence of the greater afflux of blood, while their specific gravity diminishes. Krause estimates the average absolute weight of the lungs in men to be three pounds and a half, in women two pounds and three-quarters, and the left to be smaller than the right by one-tenth. The weight, as compared with that of the whole body, is as one to forty or fifty.

In shape the lungs are adapted to that of the cavity in which they are lodged; their apices rise into the neck, their bases rest on the diaphragm, between them lies the heart with the great vessels. They are invested by a serous covering, the pleura, which, after lining the thoracic walls, is reflected over them at their root, and dips into those fissures, which serve to subdivide them imperfectly, the right into two, the left into three, *lobes*.

The *trachea* descends in the middle line from the *larynx* (which is a complicated developement of it for the protection of the orifice of the respiratory organ, and for the production of sound, and which will be afterwards described), as far as opposite the second or third dorsal vertebra, being straight, sub-cylindrical, flat behind, and about three-quarters of an inch wide. It is held permanently open by from sixteen to twenty cartilaginous rings, flattened in the direction of the wall in which they are imbedded, and deficient behind to an extent of one-third. Of these the highest is the thickest and the lowest is adapted by its shape to the bifurcation of the trachea into the two bronchi. The free ends of these cartilages are sometimes forked, and contiguous ones are now and then joined. They are immediately invested with perichondrium, a dense, white fibrous, inelastic, membrane, and are connected by a continuation of it extending between their borders and ends. This inelastic membrane, by its toughness, resists undue extension in the longitudinal direction.

Looking on the trachea behind, we observe the space between the ends of the cartilages covered with irregularly interwoven

fibres, in the course of which we have discovered unstriped muscular fibres to occur, especially about the bifurcation. In this fibrous layer are recesses for the tracheal glands, and on dissecting it off these glands are exposed, together with a thin sheet of transverse unstriped fibres, completing, as it were, the circle of the cartilaginous rings, and known as the *trachealis muscle.* The fibres of this are attached a little way from the extremities of the cartilages on their inner surface, and in contraction must serve to approximate them, and thus to narrow the canal. In the horse, they are inserted three-fourths of an inch from the extremities, which almost or quite overlap. In birds they are composed of striped fibres.

The cartilages, their interspaces, and the trachealis muscle are lined by a thin layer of longitudinal elastic anastomosing fibres, uniformly spread out except over the trachealis muscle, where they are gathered up into longitudinal bands, sometimes one-twelfth of an inch thick, very visible through the mucous membrane. These take a serpentine course down the bronchi, and preserve their anastomosing character. The trachea owes its elasticity in the longitudinal direction to the fibres now described.

The mucous lining of the trachea, the essential part of the duct, to which the above are accessory, is continuous through the glottis with that of the pharynx, and physiologically with the respiratory compartment of that cavity, and with the nasal passages (see ante p. 185). It is covered with ciliated epithelium, and the direction of the movement is probably upwards towards the glottis. The *tracheal glands* are productions of this membrane, and appear as a layer of reddish, distinct granules, behind the trachealis muscle, each one being furnished with a separate duct, traversing first the muscle and then the layer of longitudinal elastic fibres, to open on the inner surface of the tube. These glands appear to be tubular, not follicular, and are thus related rather to the sudoriferous than to the salivary system. They probably furnish much of the halitus of the breath and may determine its odour.

Of the *bronchi* or primary subdivisions of the trachea, the right is the shorter, wider, and more horizontal; the left longer to pass under the aortic arch. Their walls resemble those of the trachea with slight modifications. At the root of the lung, each breaks up into branches corresponding to the lobes (*lobal bronchia*), and these again into *secondary*, *tertiary*, and *terminal* bronchia, the last named being from one-fortieth to one-sixtieth of an inch in diameter. The terminal bronchia pass to portions of the pulmonary

substance more or less distinctly mapped out by areolar tissue and termed *lobules*.

Coats of the Bronchia.—All these become gradually thinner as they approach the air-cells. The cartilaginous pieces, which are irregular in shape and position in the lobal bronchia, become reduced to mere flakes, and finally cease in those of one-sixth or one-tenth of an inch in diameter (fig. 204). The last are seen mostly where branchings occur. The muscular fibres of the trachea are continued down even to the terminal bronchia, but instead of filling up only the gap in the cartilaginous framework, they form a uniform layer encircling the canal, but excessively thin. The fibres are here arranged in anastomosing bundles (fig. 203). Within the muscular layer is that of the longitudinal elastic fibres, here disposed as an even layer, and representing the submucous areolar tissue. The ciliated epithelium and the basement membrane of the mucous tissue both descend into the terminal bronchia. On the exterior of the bronchia is some areolar tissue separating them from the neighbouring masses of air-cells, and associated with the arteries, veins, lymphatics and nerves belonging to the bronchial wall.

Fig. 203.

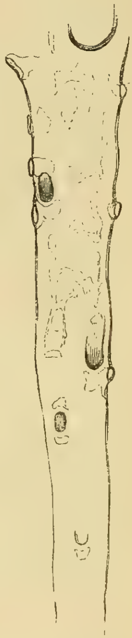
Small bronchial tube laid open, showing the transverse plexiform arrangement of the muscular layer, and its disposition at the orifice of a branch. From a man æt. fifty. Magnified 2 diam.

The *bronchial arteries* are usually two, coming from the aorta, but irregular. They supply the coats of the bronchia, and have corresponding veins. Their capillaries anastomose with those of the pulmonary artery where the terminal bronchia become lobular passages. The distribution and actions of the pulmonary nerves have been already discussed (pp. 120, 124-7).

Ultimate Pulmonary Tissue.—*Lobules.*—In some parts of the exterior of the lungs, particularly near the borders, and in some animals throughout, may be noticed a sort of mapping out of the pulmonary substance into small polyhedral masses separated by areolar tissue, and having a very irregular shape. These are the *lobules* of the lungs. They can only be made out in certain situations, even by dissection, for it does not appear that the whole human lung is thus subdivided by areolar septa. Nevertheless, it seems certain that each terminal twig of the bronchus is in relation with only its own proper set of air-cells, and that such sets of cells do not communicate except through the medium of the bronchia. In this sense lobules exist everywhere, even when not isolated by areolar tissue, and in this sense we shall use the term, as con-

veniently designating that series of air-cells, associated by dependence on a single terminal air-tube. We shall afterwards show how much difference exists in the isolation of the lobules of the *liver* even in allied animals, and how unimportant this variety appears to be.

Fig. 204.



Small bronchial tube laid open, showing the arrangement of the last cartilaginous flakes. The tube has been cut across above, at the point where it penetrates the substance of the lung, and below where it has a diameter of about 1-12th of an inch. The elastic and muscular fibres are not represented, but both were so delicate as to allow the adjacent air-cells to be seen through the bronchial wall. Ciliary epithelium was traced in the finest tube that could be opened by scissors, viz., of 1·40th inch diameter. From a healthy man æt. twenty-five. Natural size.

The superficial lobules derive a covering on one aspect from the pleura, but are separated from it by rather dense areolar tissue, which may be dissected off without rupturing the air-cells. If the interstices between contiguous superficial lobules be explored by the knife, the terminal bronchia are found at the bottom of the fissures, each going to a single lobule, and besides these are seen branches of the pulmonary artery and vein, not running in company, nor limiting themselves to a single lobule, but common to contiguous lobules; so that the air-spaces of one lobule do not communicate with those of another across the interstices, but the blood-vessels do. On the exterior of a lobule we observe bubbles of air of various sizes in its tissue, and if the bronchial tubes be injected, the lobule is distended, and its exterior presents a number of bulgings known as the *air-cells*, about which much controversy has existed. Their shape seems irregularly polyhedral, like the lobules themselves. The angles, where three or more of these cells meet, are the points at which the terminal twigs of the pulmonary artery and vein penetrate among the cells, after meandering more or less over the surface of the lobule. In their course in the interior of the lobule, these twigs generally run separately in the lines of junction of three or more cell-walls, branching as they run and breaking up into their capillaries on either hand.

As the superficial lobules are truncated where they form the surface of the lung, so the cells are truncated where they form the surface of the lobule. This is most decidedly the case where the lobules are well defined, and admit of separation; but where contiguous lobules are not isolated by areolar tissue (as in most parts of the interior of the lungs, and in the lungs of the smaller

mammalia), their superficial cells have their inequalities mutually adapted to each other, and even their walls fused together, so that the lobules would not remain distinct, were it not that their air-cells do not communicate across the interval.

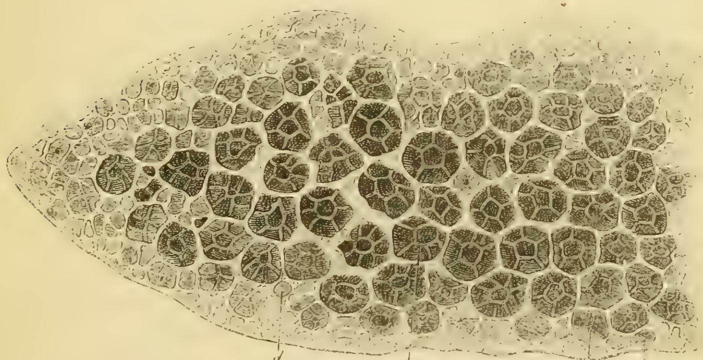
To convey a correct, and at the same time a simple, idea of the constitution of the pulmonary lobules, we must regard each as an elementary lung, perfect in itself as an arrangement of a respiratory membrane adapted to the aeration of the blood. First, the terminal bronchial tube pertaining to each lobule, loses its epithelium and muscular tunic at about one-eighth of an inch distant from the last air-cell to which it leads, and is thus reduced to basement tissue and yellow elastic fibres, which become blended into a single coat, the only membrane composing the tubes beyond, and the air-cells. The terminal bronchial tube, thus simplified, ramifies within the lobule, and its branches may be conveniently distinguished from the bronchial tubes under the name of *lobular passages.** The lobular passages are wider than the terminal bronchia, and are remarkable (being honeycombed on their interior) for presenting a series of sacculi or cells on their wall. These are the pulmonary *air-cells.* They form a number of bulgings of the wall, and are separated from one another by septa projecting inwards from the wall towards the axis of the passage (fig. 206). They each open separately into the lobular passages, and do not communicate with each other except through the passages. The terminations of the several lobular passages are air-cells coming up to the surface of the lobule, but some of the air-cells placed laterally on the passages, also contribute to form the surface of the lobule. The air-cells thus surround and terminate each lobular passage — and the lobule consists of a number of lobular passages, associated by their dependence on a single terminal bronchial tube, and each clothed as it were, on its sides and at its end, with a honey-comb of air-cells, with orifices open towards the cavity of the passages. Contiguous cells of the same passage are separated by a simple septum or process of the wall, while the contiguous cells of neighbouring passages are separated by a septum, likewise simple, formed by the union of the walls of each. Where the septa spring from the wall of the passage, or in the angles where neighbouring cells unite, the wall is strengthened by a greater thickness of elastic tissue, which often has the form of arching bands of considerable strength in these situations, as well as around the orifices of the cells. Thus the lobular passages and the air-cells are formed of one tissue, and

* Dr. W. Addison, Phil. Trans. 1840.

perform the same function. They are a series of branched cellulated air-passages, not lined with epithelium, or coated with muscular tissue, but highly extensible and elastic, of much larger aggregate capacity than the terminal bronchia which lead to them, and resembling closely, in general conformation, the reptilian lung. Indeed, an admirable notion of the essential arrangement of the lobules of the mammalian lung may be derived from an examination of the terminal parts of the sacculated bronchia of the lung of the turtle. The lobular passages are wider than the terminal bronchia of which they are the continuations, and than the cells which pullulate on their walls. They also branch again and again in order to spread from the terminal bronchial tube on every hand throughout the whole area of the lobule, and as their ramifications observe no certain order or course, it happens that sections carried through the lobules are rarely found to follow any single passage far, so as to display, in a happy manner, its mode of distribution. Sometimes, however, this is better seen than at others.

M. Rossignol has recently given an elaborate description of the pulmonary structure. He insists particularly on the ultimate bronchial ramifications being in shape like an inverted funnel, and he terms them the *infundibula*. The cells, forming a honeycomb on their interior, he calls the *alveoli* (figs. 205 and 206). Emphysema,

Fig. 205.



Thin slice from the pleural surface of a cat's lung, considerably magnified. At the thin edge, *b c d, alveoli* are seen. In the centre (as *a*) where the slice is thicker, alveoli are seen on the walls of *infundibula*. *From Rossignol.*

according to this author, seems to consist in a distension of the passages and cells, and a breaking down and obliteration of the septa, first between the cells of the same passage and then

between neighbouring passages, and even between contiguous lobules.

The diameter of the lobular passages is from $\frac{1}{100}$ to $\frac{1}{200}$ of an inch; and that of the cells from $\frac{1}{200}$ to $\frac{1}{300}$ of an inch according to our measurements. In a preparation of the lung of the calf, given us by our friend Professor Retzius, they measure $\frac{1}{600}$; and Dr. W. Addison makes them from $\frac{1}{200}$ to $\frac{1}{500}$ of an inch.

Fig. 206.

Bronchial termination in the lung of the dog. *a.* Tube (lobular passage) branching towards the infundibula. *b.* One of the infundibula. *c.* Septa projecting inwards on the infundibular wall and forming the alveoli, or cells. *From Rossignol.*

The skeleton of the lobule is thus an elastic membrane elaborately arranged, so that the air may be brought into contact with it for the most part on both its surfaces. Over this membrane the whole venous blood of the body is made to course in a continual stream so as to be submitted to the action of the air.

Vascular Element.—The *pulmonary artery*, conveying the venous blood to the lungs, is about as large as the aorta, and is furnished with a triple valve at its origin from the right ventricle of the heart. It soon divides into a right and left branch, which enter the lungs at their root and ramify as far as the lobules in company with the bronchia. Arrived at the lobules, the small branches of the pulmonary artery do not enter in company with the lobular passages, but distribute themselves over the lobules in the interlobular fissures, penetrating at various points between the air-cells, and occupying tubular channels in the angles where three or more cells meet. These channels are formed of the same yellow elastic tissue which constitutes the lobular passages and air-cells, and their wall blends with the proper coat of the terminal twigs of the pulmonary artery which occupy them. The capillaries of the lobule are given off both from the twigs which meander over the lobule and from those which penetrate it, and they form a network which covers the walls of all the cells of the lobule, as well as of the lobular passages, anastomosing with some twigs of the bronchial arteries where the passages are continuous with the terminal bronchia. This network empties its blood into venules which lie first in intercellular channels similar but intermediate to those which lodge the arterial terminations; and these venules collecting the now aerated blood from the interior and also from the surface of the lobules, converge to larger veins which lie in the interlobular spaces and tend towards the root of the lungs, but for the most

part by a route distinct from that of the arteries and bronchia. Thus the general mass of the lung may be regarded as containing two series of ramified canals, one transmitting the bronchia (with their vessels and nerves) and the pulmonary arteries, the other the pulmonary veins. This interesting fact was well described by Dr. Addison, of Guy's Hospital, in a paper in the Medico-Chirurgical Transactions in 1840. At the root of the lungs four pulmonary veins result, which forthwith discharge their torrent of arterialized blood into the left auricle of the heart.

The cause of the separate course of the pulmonary arteries and veins is to be found in the opposite position of their radicles, in regard to the capillary network of the lobules, it being a convenient arrangement for the terminal arterial and venous twigs to hold alternate positions among the capillary network, so that each arterial twig disperses its blood in all directions, and each venous radicle collects it from all sides. An obvious analogy exists in respect of the course of the vessels and ducts between the liver and lungs, the bile ducts answering to the air passages, the hepatic artery to the bronchial arteries, the vena porta to the pulmonary artery, the hepatic vein to the pulmonary vein. The nerves and lymphatics pass in both cases with the ducts.

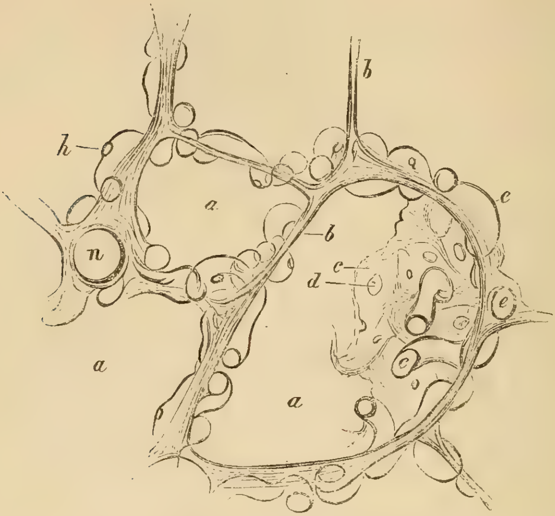
The capillary network of the lungs lies on and in the walls of the air cells and lobular passages. These walls are for the most part much too thin to enclose the capillaries between two layers of their substance, and therefore the capillaries project fairly into the air cells, by a great part of their circumference, being adherent to the wall by a narrow line only. The capillary wall is thus exposed and bare, in contact with the air of the cell, and nothing besides the delicate membrane of the capillary intervenes between the air and the blood. A capillary frequently passes through an aperture in the cell wall, so as to project first into one cell, and further on into a contiguous one, but never becomes altogether free from the wall. In passing, its wall is blended with that of the cell. The nuclei seen in the capillary walls elsewhere are very conspicuous in those of the lungs.

The best way of proving the arrangement of the capillaries is by injecting a lung with size by the pulmonary artery till the blood-vessels and the air cells are both filled, the latter by transudation, and then slicing it when cold. The capillary wall is then seen to be uncovered by any tissue, just as is usual in the Malpighian tufts of the kidney. The diameter of the capillaries is about $\frac{1}{1800}$ of an inch, which is large, and the blood therefore passes freely. The

meshes of the network are not much wider than the vessels themselves.

Mr. Rainey says that on the surface of the lung, the capillary

Fig. 207.



View of a thin section of the lung of a cat, which had been injected by the pulmonary artery with gelatine, so as to fill blood-vessels and air-cells, and had been sliced when cold. *a a a.* Air-cells and lobular passage in section. *b b.* Their wall in section. *c.* Their wall in face. *d.* Extremely faint nucleus in the same. *e e.* Capillaries. *h.* Nucleus in wall of capillary. *n.* Small pulmonary artery or vein with simple wall. Magnified 250 diameters.

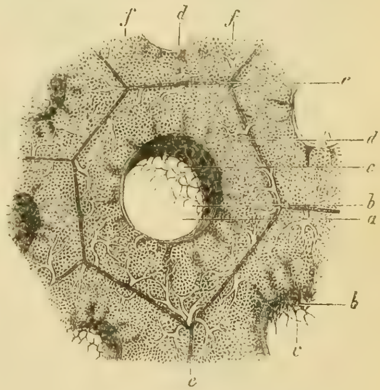
network extends over a space corresponding to not more than ten or twelve cells, *i.e.* over from one-thirtieth to one-twentieth of an inch, and if the rate of the blood be taken at an inch and three quarters per minute, according to the estimate of Valentin, drawn from observation of the frog's foot, the blood would be somewhere about one second and a half in contact with the air at each circuit. But probably in the higher animals its transit is more rapid.

We may here refer to some very interesting observations on the arrangement of the capillaries and terminal air passages, lately made by Mr. Rainey. This careful and accurate anatomist was the first to insist on the fact that, in mammalia and birds at least, the capillaries are, as we have above noticed, *bare;* exposed on their exterior to the air, not covered by any membrane, either mucous or serous, or by any epithelium; and that by this arrangement the most perfect aeration of the blood which traverses them is provided for. The air and the blood may be said to be in contact through the delicate capillary wall, a film less than $\frac{1}{20000}$

of an inch in thickness. In some of the mammalia, as the kangaroo, the rat, and mouse, the terminal air spaces are too minute to contain even a single particle of epithelium, and cannot therefore be lined by a pavement of such particles. The elastic tissue described as forming the cell wall in the human lung, is in such instances very imperfect, being deficient in the areolæ of the vascular network, so as to render the cell-walls cribriform, or rather to reduce the terminal air-receptacles into a congeries of inosculating and most minute and irregular passages.

In the bird's lung the elastic tissue, according to the same anatomist, is even more scanty. The mucous membrane lining the bronchia, ceases at the commencement of the lobular passages, and these passages seem hollowed out in the substance of a solid capillary plexus, or one in which the capillaries extend and anastomose indifferently in all directions. This vascular plexus forms the only wall of these passages, and the air has access from the passages into the interstices of the plexus, so as everywhere to surround and touch the whole surface of every capillary. Instead therefore of the terminal air-spaces being cells with a plane network of capillaries on their walls, they are the mere interstices of a solid vascular plexus. Thus a more abundant intermixture of the blood and air is secured, and the ultimate tissue of the lung is reduced to the simple capillary wall, arranged so that air has access to its exterior. The adhesion of the lungs to the costal surface, and the support afforded by the cartilaginous and other tissues of the bronchial tubes, as well as by the areolar tissue bounding the elongated lobules, are sufficient to maintain the integrity of so frail a web. The aerial interstices of the vascular plexus are usually even smaller in diameter than the capillaries themselves, and, according to Mr. Rainey, average $\frac{1}{9600}$ of an inch. The above fig. (208) is from

Fig. 208.



Slightly oblique section through a bronchial tube. Showing at *a* the cavity of the tube. *b*. Its lining membrane, containing blood-vessels with large areolæ. *c c*. Perforations in this membrane, where it ceases at the orifices of the lobular passages, *d d*. *e e*. Spaces between contiguous lobules, containing the terminal pulmonary arteries and veins supplying the capillary plexus, *f f*, to the meshes of which the air gains access by the lobular passages.

Mr. Rainey's paper, and is drawn from the lung of the fowl, highly magnified.

The gradations of perfection in the respiratory surface, considered as to its minute organization in Reptiles, Mammalia, and Birds, may be thus recapitulated.

In *Reptiles* the cells are large and few. The air has access to the respiratory capillaries only on one surface, viz., that towards the cavity of the cell which they line; and where two cells are contiguous, but separated by a septum, the septum has a capillary web on each of its surfaces.

In *Mammalia*, for the most part, the cells are much multiplied, and where two lie side to side, the septum between them has but one layer of capillaries, which is, in a great measure, common to them both, and aerated on both its surfaces. And here we may remark the reason of the non-isolation of the lobules by areolar tissue in the mammalian lung, except at the borders and thinner parts, where such isolation is necessary for the movements of the lung in respiration. When the lobules are thus isolated, the capillaries on the cell-walls which bound the lobule, can have air only on that surface which is towards the cavity of the cells; whereas, when the contiguous lobules are blended by the fusion of the cell-walls which form their exterior, these cell-walls, like the rest, contain but a single respiratory plexus, which is aerated on both its surfaces.

In *Birds* the respiratory capillary plexus is rendered the most perfect possible, both by the omission of the elastic supporting tissue, and also by the vascular plexus being no longer lamellar but solid, or extended alike in all directions. It is manifest that by this arrangement, a given pulmonary space is made to contain the greatest possible quantity of capillary wall, and that this wall is exposed most completely to the action of the air admitted around it.

Movements of Respiration.—The thorax is a moveable framework composed of a nearly fixed column, the dorsal spine, on which are moveably articulated twenty-four ribs, curved and inclined, so as to embrace a large conical space, and ending in cartilages, which with three exceptions on each side (the floating ribs) are joined in front through the medium of a flat piece, the sternum, the inclination of which is downwards and forwards. The upper orifice, embraced by the vertebral column, first ribs, and sternum, is closed by a fascia of dense areolar tissue, rendered extremely irregular by the apices of the lungs, rising slightly into the neck, and by the various structures, the œsophagus, trachea, great blood-vessels, muscular and other parts, that pass through it. The lower orifice, which is very much larger, is closed by the diaphragm, an arched and sloping musculo-tendinous septum between the thorax and abdomen, through which pass the inferior vena cava, the aorta, and great absorbent trunk, as well as the œsophagus and the pneumogastric and sympathetic nerves. Between the ribs are placed the two layers of intercostal muscles with oblique fibres oppositely crossing, and chiefly on the exterior of the bony framework

are added other muscles, which may enlarge or diminish the area of the cavity, and thus act in respiration, but which are, for the most part, subservient to the general muscular movements of the body.

The thorax is capable of enlargement in all its dimensions, in height, depth, width. Its vertical extent is increased by the elevation of the ribs and the widening of the intercostal spaces, but chiefly by the descent of the diaphragm. Its antero-posterior and transverse diameters are increased by the elevation of the ribs, which carry forwards as well as raise the sternum (and the lower end of that bone usually a little more than the upper, in consequence of the greater length and obliquity of the lower sternal ribs), and which also seem to undergo a slight rotation on a line joining their two extremities, by which their middle part is raised and slightly removed from the median plane of the thorax. These are the principal modes provided in the mechanism of the thoracic walls, for its dilatation in breathing. It should be added that during the advance of the sternum the arch of the ribs is widened, chiefly by a torsion of their cartilages, and that the elastic rebound of those parts is a powerful agent in expiration.

Fig. 209.

Diagrams showing the extent of antero-posterior movement in ordinary, and forced respiration in male and female. "The back is supposed to be fixed, in order to throw forward the movement as much as possible" The black line indicates, by its two margins, the limits of *ordinary* inspiration and expiration. In *forced inspiration*, the body comes up to the dotted line, while in *forced expiration*, it recedes to the smallest space indicated. From Dr. Hutchinson.

Observed Movements.—All the foregoing modes of enlargement of the thorax act in deep inspiration, but in ordinary breathing, there are considerable differences according to sex and age. In men an ordinary inspiration is attended with very slight elevation of the ribs, not more than one-twentieth of an inch, according to Dr. Hutchinson's

observations; whereas in women, this movement is very obvious, particularly in the upper ribs. It is not improbable that the cause of this may lie in the narrower waist of the female, obliging an undue enlargement of the upper part of the thorax to compensate for the smaller size and less dilatability of the ample base. The separation of the ribs and widening of the intercostal spaces when the chest is enlarged, are proved by measurement both in the living and dead. Dr. Hutchinson has made casts of the interior under both states. Dr. Sibson divides the ribs into three sets, a superior set of five separately joining the sternum, an intermediate set of three, with conjoint cartilages, and an inferior or diaphragmatic set of four with floating cartilages. He considers that all, except the upper four in their front part, diverge from one another in inspiration, the inferior set the most, but the lowest of all remaining stationary. Messrs. Beau and Maissiat* describe three varieties of ordinary respiration: 1. Abdominal, or that chiefly effected by the diaphragm, and apparent in the motion of the abdominal walls. This occurs in infants up to the end of the third year, and in males generally. 2. Costo-inferior, or that in which the lower ribs (those of Mr. Sibson's intermediate and inferior sets) are observed to act. This is observed in boys after three, and in men. 3. Costo-superior, or that effected in a considerable degree by the upper ribs. This is observed in females, especially in adults.

Action of Muscles.—The *diaphragm* has an arched form, is highest in front, lowest behind. The fibres pass to a central tendon on which is seated the heart in the pericardium, the lungs resting chiefly on the muscular parts. Its contraction would tighten and then depress both the central tendon and the muscle generally, and would also tend to straighten the curves formed by the fibres as they pass from the spine and ribs to the central tendon. Thus the heart would be lowered a little, but, perhaps, the lungs more, and the area of the pulmonary compartments of the thorax would be much enlarged, for the diaphragm acts at their wide and ample base, where a slight range of vertical movement produces a great effect. In its descent the diaphragm presses down the abdominal viscera, and bulges the abdominal walls. In expiration it recedes upwards, being pushed upon by the abdominal walls through the medium of the viscera.

The action of the *intercostal muscles* is less obvious, and had been the subject of much difference of opinion, even before the days of Haller. It may be studied on mechanical principles, and by obser-

* Archiv. Gén. de Méd. t. xv. p. 399.

vation. Hamberger * has given the most elaborate and complete exposition of the mechanical view of the subject, and has illustrated it with diagrams and models. He shows that if two parallel bars (ribs) slope downwards from a fixed vertical column (spine) to which they are separately articulated (heads of the ribs), and are kept separate at their opposite ends (as by the sternum), then a contractile force (muscle) acting between them, will raise or depress both bars, according to the direction of its obliquity. If the contractile cord slope downwards *from* the column representing the spine (external intercostal fibres) the bars will both be elevated by its contraction, and will carry upwards the sternal element. As they rise the cord is seen to shorten.

If on the other hand the contractile cord slope downwards *towards* the vertical column (internal intercostal fibres) then the bars will be both depressed by its contraction. It is obvious that the space between the bars will be widened as they rise towards the horizontal line, and narrowed as they fall. Hence it seems clear, without entering upon the mechanical theorems by which the above results may be proved, that the action of the external and internal intercostals must be antagonistic. That the former must elevate and open out the ribs, the latter depress and approximate them—that as the fibres of the one are shortened those of the other must of necessity be lengthened.

It is true that the ribs are curved, and variously flexible, instead of straight and stiff; that their articulations differ from one another, and are nowhere purely ginglymoid, and that other forces besides the intercostal muscles influence their movements.

These considerations, however, do not seem to affect the substantial accuracy of Hamberger's views, so far as relates to the greater number of the ribs, and indeed to all in the posterior region. And Dr. Hutchinson has done well to call attention to them and to illustrate them by new researches. But Dr. Sibson has shown by observations both in man and animals, and in the latter especially, by a series of careful experiments upon the actual movements of the thoracic walls and their muscles, exposed during life, that the external intercostals are not everywhere inspiratory, nor the internal ones expiratory. For, in the upper two or three spaces in front, the internal, as well as the external intercostal fibres, contract and approximate the ribs. Those fibres, also, of the internal intercostals which pass between the cartilages of the ribs contract during inspiration, and correspond with the internal intercostals of the

* Physiologia Medica, Jenæ, 1751, 4to. p. 140, *et seq.*

sternal ribs of birds, which are powerfully inspiratory, and slope downwards and backwards from the sternum. These may have their action explained by Hamberger's views, if the sternum be regarded as giving the fulcrum instead of the vertebral column. Again, the lowest external intercostal lengthens in inspiration, and is an expiratory muscle, the eleventh rib in inspiration rising from the twelfth, which is stationary.*

On the whole we may conclude, that in inspiration, the upper ribs rise by the action of the scaleni—that the rest of the ribs in their hinder part rise and open out by the action chiefly of the external intercostals; while in front the intercostal spaces are narrowed above by the rise of the second, third, and fourth ribs towards the first, and at the same time widened midway and below, the flexibility of the costal cartilages having much to do with this latter movement. It may, also, be regarded as certain that the internal intercostals, except in front, are muscles of expiration, and approximate the ribs.

Dr. Sibson has well pointed out that the forces which expand the thorax act, in a great degree, in a separate and independent manner on its several parts, that the lower region, and the lower lobes of the lungs which fill it, are enlarged by the diaphragm and lower external intercostals, while the upper region expands under the influence of the scaleni, its external intercostals, and (in front) its internal intercostals. A variety of morbid conditions of the lungs, where the expansibility of one or more lobes is modified, illustrates this observation, for one side of the chest may be observed to expand without the other, or a portion of one side without the rest. How important this amount of independence of the parts of the chest is to the preservation of life, under accident or disease, needs hardly be explained.

* On February 26, 1851, Dr. Sibson exposed the intercostal muscles in a dog under chloroform, when we noted the following as facts :—1. The lower fibres of the serratus magnus contract during inspiration; the upper fibres lengthen. 2. The first five intercostal spaces diminish *decreasingly* during inspiration. 3. The seventh, eighth, and ninth ribs diverge *increasingly* from the seventh to the ninth, and the tenth, eleventh, and twelfth in a less degree. 4. The twelfth rib is stationary. 5. The first external intercostal muscle shortens, the lowest lengthens, during inspiration. 6. The first and second internal intercostal muscles, in front, shorten during inspiration; the third, also, in a very slight degree. 7. The sixth internal intercostal elongates during inspiration, and the ninth also, but in a greater degree. 8. The eleventh anterior external intercostal of the diaphragmatic ribs shortens during inspiration. 9. Behind, the tenth external intercostal shortens, the tenth internal lengthens, during inspiration.

In addition to the muscles now mentioned, the *levatores costarum*, *cervicalis ascendens*, and *serratus posticus superior*, are probably muscles of ordinary inspiration; and those of the abdominal wall, with the *levator ani*, of expiration; the latter action being aided by the elasticity of the ribs and their cartilages, and by the resilience of the elastic tissue entering so largely into the composition of the lungs themselves. This resilience (which Dr. Carson showed to be sufficient in sheep and dogs to balance a column of water from one to one foot and a half in height) occasions the collapse of the lungs when the pleural cavity is accidentally opened, as sometimes by wound of the parietes. In such cases the air passes in and out of the thorax through the wound in respiration, and the air previously in the lung is expelled through the glottis by the elastic force of the pleura and walls of the air-passages and cells. If the lung also be wounded, the air may pass into the pleural sac from the air-passages under the same resilient force, and be thence pumped by the expiratory forces through the wound in the parietes into the areolar tissue of the body, as so often happens in the case of fractures of the ribs.

Extraordinary Muscles of Respiration. — In voluntary deep breathing, or when (as in asthma) the head, neck, and upper extremities become fixed points for the muscles passing between them and the thorax, the lower part of the serratus magnus, the pectorales, the subclavii, with the sterno-mastoidei, trapezii, and some others, aid in dilating the chest. Some difference exists among the most recent authors as to the share particular muscles take in the movements of respiration; and this is not surprising when we consider the complexity of the problem, the difficulty of determining the fixed points, or of observing the muscles in separate action. In *forced expiration*, the triangulares sterni, the serrati postici inferiores, sacrolumbales, latissimi dorsi, with their accessories as high as the highest costal insertion, probably help to depress and approximate the ribs.

Power of the Respiratory Muscles.—Dr. Hutchinson has lately made numerous experiments on this subject, and his results and those of Valentin and Mendelssohn agree. He finds as the average of 1500 trials that the expiratory power exceeds the inspiratory by one-third; that men of 5 feet 7 or 8 inches have the greatest inspiratory power, and should on an average raise a column of mercury three inches; while, above this, the strength gradually decreases as the stature increases, so that a man of 6 feet raises a column of only two inches and a half: also, that occupation or mode of life serves much

to modify the relation which the inspiratory and expiratory powers bear to each other. Thus, wrestlers, boxers, and others, accustomed to employ the extraordinary muscles of respiration, in rendering the thorax a fixed point from which other muscles might act, were found to have an unusual power of expiration. In one wrestler he found the expiratory power exceed nearly four times that of the natural inspiratory power. Valentin in six experiments on young adult males found the force exerted in *ordinary, tranquil* inspiration and expiration to be from about one-seventh to three-sevenths of an inch of mercury. Dr. Hutchinson calculates that a man who raises three inches of mercury by an effort of inspiration exerts a force equal to 1000 lbs. In one man he found the mercury raised to such a height (seven inches) as to indicate a force of 2200 lbs., or nearly two tons.

When the capacity of the thorax is augmented, the air in the lungs expands so as to keep them in contact with the walls, and the external air enters by the trachea to restore the equilibrium. When the dilating force ceases, the walls of the chest contract upon the lungs, and expel a portion of the air, the lungs themselves conspiring.

Use of the Trachealis Muscle.—That the trachealis in contracting must diminish the area of the trachea and bronchia is obvious from its arrangement no less than from experiment. Dr. Williams found that the lungs taken from an animal just killed manifestly contracted under the stimulus of galvanism. The fibres are allied to those of the ducts of glands, and of the blood-vessels, and are consequently probably incapable of coinciding in action with the muscles of respiration. It further seems impossible to assign an object to any peristaltic action which might be attributed to them. We are disposed to consider that the trachealis muscle contracts and dilates the air-tubes slowly, in relation to the activity of the respiratory function at different times of the day, or under other modifying circumstances. Its contraction would tend to limit the quantity of air transmitted in a given time, or would quicken its passage. It is in all probability contracted spasmodically in spasmodic asthma, and in the early stages of bronchitis. If it contracts during the sensation that precedes and accompanies coughing, this would facilitate the expulsion of mucus by quickening the expelled current of air.

Excitation of the Respiratory Movements.—We have already referred to the share taken by the nerves in respiration. The respiratory acts are essentially involuntary, and unconsciously performed,

although we have a limited power of checking or accelerating them, of varying their rhythm or force, and can become aware of them by an effort of attention. After holding the breath for fifteen or twenty seconds during ordinary respiration, or forty seconds after a deep inspiration, there arises an insupportable sensation over the whole chest, concentrated under the sternum, and no effort can maintain the interruption of the respiratory acts. This urgent sensation of want of breath when carried to its full extent by any mechanical impediment to the aeration of the blood, is one of the most painful and oppressive kind, and is referable to the pulmonary plexuses distributed on the bronchia, and perhaps on the walls of the lobular passages and cells. The impression made on these peripheral nerves by the absence of oxygen, and the undue presence of carbonic acid in the air in contact with them, is propagated to the spinal cord and medulla oblongata by the sympathetic and vagus, and there excites those combined actions of the muscles of inspiration which lead to the renewal of the air; and it may be fairly concluded, that the ordinary motions of respiration depend on the same circle of nervous actions, which thus voluntarily arrested, become apparent by their accumulated force. (See *ante*, p. 124). The muscular actions of expiration, which seem to follow so evenly on those of inspiration, are probably due, in part at least, to the stimulus of elongation of their fibres. When the ribs diverge, the fibres of the internal intercostals, except in front, are extended.

Frequency of Respirations and Ratio to the Pulse.—The number of respirations per minute in healthy adults is from eighteen to twenty, but according to Dr. Hutchinson's observations on more than 1700 persons (when sitting) the range in health may be from six to forty, though most persons breathe from sixteen to twenty-four times per minute. The proportion which the respirations bear to the beats of the heart is liable to much variation, but is in general not far from that of one to four. Dr. Guy has shown that the respirations are rather more frequent in the evening than in the morning, whereas the pulse is rather slower. He has also discovered that the proportion between the respirations and pulsations is much deranged by changes of posture, probably by these modifying the expansion of the lungs at each inspiration, without inducing any corresponding change in the transmission of the blood.

Aerial Capacity of the Lungs, and Amount of Air breathed.—When the lungs have been emptied as much as possible of air by a forced expiration they still contain a residual quantity, which may be estimated at about forty cubic inches. The mechanical

conditions under which the organs are placed do not allow of their expelling this remnant. If now the deepest possible inspiration be taken it is found that they are capable of inhaling a further quantity, varying much in different persons, but on an average about 240 cubic inches, which, with the former residual quantity, make a sum of 280 cubic inches as the full capacity of the lungs of a person of good height (5 feet 8 inches). But in ordinary breathing the lungs are neither very empty, nor very full — they maintain a middle condition, and their range of movement in natural or ordinary respiration, is only sufficient to pump in and out a quantity of air equal to about 30 cubic inches. From the best observations it may be concluded, that a person whose full capacity is 280 cubic inches, contains in his lungs, after an ordinary expiration, about 110 cubic inches; and after an ordinary inspiration about 140 cubic inches, a quantity which he is enabled to double by a *full* inspiration. Thus rather more than one-fifth of the ordinary contents of the lungs are expelled at each expiration, and again renewed by inspiration.

Dr. Hutchinson, by means of a gasometer, which he terms a *spirometer*, has examined a large number of persons with reference to their power of taking air into the lungs. The person first inspires to the full extent, and then breathes into the instrument as much air as he can, and it results that the *height* of the individuals has much to do with their respiratory range. Thus, while on an average a person of 5 feet breathes 174 cubic inches; one of 5 feet 1 inch will breathe 182 cubic inches, and for every inch of height up to 6 feet will breathe about 8 cubic inches additional. Weight has much less influence than height, but tends to diminish the respiratory power when beyond a certain limit. In males of the same height, the respiratory range (*vital capacity* of Hutchinson) increases from 15 to 35 years of age; but from 35 to 65 it decreases nearly $1\frac{1}{2}$ cubic inches per year. Bourgery agrees nearly with this: he states that more air can be inspired at thirty than at any other age, and that in old persons the range is very limited. Bourgery calculates that a child of ten years of age, with a weight three times less than that of a man of eighty, has a respiratory power eight times greater. This is due to the great difference there is in the range of the respiratory movements. The old man being able to increase the amount breathed by less than a half, while the child may increase it nearly fourteenfold. Herbst has shown that the capacity of the lungs is much smaller in the female than in the male.

Having now considered the anatomy of the respiratory organs,

and the movements which regulate the supply of air, we may proceed to consider the changes which occur in the air during its sojourn in contact with the respiratory surface, and also the corresponding changes in the blood circulating there.

Changes in the respired air.—The air consists of a mixture of oxygen and nitrogen, in the respective proportions of about 20·81 and 79·19 in 100 parts by volume, with the addition of a very minute portion of carbonic acid gas, not exceeding one part by volume in 2000. It contains watery vapour in variable quantity, according to temperature and other circumstances; and also non-estimable quantities of other gaseous and volatile substances, of no account in relation to the respiratory function. In air that has been breathed, the temperature is found to have assumed nearly or quite that of the blood, the quantity of moisture has nearly reached the point of saturation, the proportion of oxygen has diminished, and that of carbonic acid has increased, while that of nitrogen has slightly increased, or has undergone little change. A small quantity of animal matter has also been received from the air-passages, as is proved by the brown colour assumed by sulphuric acid, through which the respired air is made to pass.

Aqueous vapour exhaled.—It results from the most careful experiments, amongst which may be mentioned those of Valentin and Brunner, and of Moleschott, that the air expired is usually nearly saturated with moisture, and that the quantity of water thus escaping from the system in twenty-four hours, may be estimated in temperate climates at from twelve to twenty ounces. It is, of course, impossible to ascertain, nor is it important, how much of this quantity is derived from the respiratory surface, strictly so called, and how much from the moist and vascular surfaces of the nasal, pharyngeal, and bronchial passages.

Exhalation of Carbonic Acid by the Lungs.—It is easy to show that carbonic acid gas is exhaled from the lungs, by breathing into lime-water, which thus becomes turbid by the formation of insoluble carbonate of lime; or into a phial, where a taper is then at once extinguished.

In 100 parts by volume of expired air (as an average of many experiments),

		Carbonic Acid.
Coathupe .	found . .	4·02.
Valentin and Brunner .	,, . . .	4·38.
Vierordt .	,, . .	4·33.
Thomson .	,, . . .	4·16.

The general average of the results of Valentin and Brunner, and Vierordt, all of which were performed on adult males, may be accepted for that age and sex, viz., 4·35 parts of carbonic acid in 100 parts of expired air ; or deducting the small quantity of carbonic acid contained in the air when inspired, we may conclude that 4·30 parts per cent. by volume of that gas are derived from the lungs at each ordinary expiration. Taking, as before, 30 cubic inches as the volume of each expiration, the actual quantity of carbonic acid in each will be 1·29 cubic inches=about 23 cubic inches per minute=about 1393 cubic inches per hour=about 27,864 cubic inches, or 16·1 cubic feet per day. In this last quantity of carbonic acid there are about seven and a half ounces by weight of carbon.

A great variety of circumstances no doubt modify the activity with which carbonic acid is formed in the system, and eliminated from it ; some of these are very worthy of notice. *Digestion* has been observed to be attended with an increased exhalation of it in many of the lower animals; and Scharling, Valentin, and Vierordt have recently noted the same fact with great accuracy in Man. Thus, one hour after a midday meal, Vierordt found that his pulse was quickened by 15, his respiration by 1, the volume of the expired air was slightly increased, nearly 50 per cent. more of air, and $2\frac{1}{2}$ cubic inches more of carbonic acid were expired in one minute, and the per centage of carbonic acid in the expired air was also augmented in a very trifling degree. If the meal were omitted these results did not occur. On the other hand, *fasting*, especially if prolonged, diminishes the exhalation.

Particular substances taken into the blood, exert a very remarkable influence upon the development of carbonic acid in the system. Dr. Prout long since observed a considerable diminution under alcohol, particularly if taken on an empty stomach ; and his conclusions have been fully confirmed by Vierordt and Bocker. The former found that, having taken more than half a bottle of wine, the carbonic acid fell in a quarter of an hour from 4·54 to 4·01 per cent. of the expired air ; *i. e.*, by about one-ninth of its whole quantity ; and this lasted for two hours. In addition to this, the latter author found that, under the same influence, the whole constituents of the urine are diminished in amount. Dr. Prout states that a dose of strong tea likewise lessens the exhalation of carbonic acid.

Since the introduction of ether and chloroform as anæsthetics in the practice of surgery, their mode of action has been much inves-

tigated, and by no one more extensively or more accurately than by Dr. Snow, who has, among other matters, turned his attention to the amount of carbonic acid gas passing from the lungs under their use. A small animal being placed in a jar, in which the air could be circulated in connection with a receptacle containing solution of potash, for absorbing the carbonic acid, the quantity of this gas expired during periods of half an hour, was estimated, when the animal breathed firstly air, and afterwards air mixed with certain quantities of the vapour of chloroform. The results were such as the following;—A dog, eight pounds in weight, exhaled in air 10·1 grains of carbonic acid gas; in air mingled with 36 grains of chloroform vapour, only 4·8 grains. A half-grown cat expired in air 5·7 grains of carbonic acid gas; in air mingled with 20 grains of chloroform vapour, only 2·0 grains. And this diminution was observed, on this and other occasions, to be in spite of increased muscular efforts on the first introduction of the chloroform, such as are known to have a tendency to augment the excretion of carbonic acid.

Exercise increases the exhalation of carbonic acid, and doubtless also the formation of it in the tissues. Mr. Newport observed that the generation of carbonic acid from bees, when at rest, did not exceed that from cold-blooded animals, but when in active movement it was more energetic than in any other animals; and other experimenters have produced analogous results. With more precision, and in the case of the human adult, Vierordt shows, that, during moderate exercise, there is an average increase per minute of 19 cubic inches in the expired air, and of 1 cubic inch in the expired carbonic acid.

The *temperature of the surrounding medium* was shown by Seguin and Lavoisier to have an important influence on the exhalation of carbonic acid, and their results were corroborated by those of Crawford. Vierordt has recently examined this point also. In numerous experiments upon himself, at temperatures of which the average was 47° Fahrenheit, he expired 18·25 cubic inches of carbonic acid per minute; while at temperatures of which the average was 67° Fahrenheit, he expired only 15·72 cubic inches in the same period. At the lower temperature, the number of respirations was increased, and more air was expired in the proportion of 406 to 366, or about 10 to 9. Cold, therefore, contrary to what might have been expected from its depressing effects on the system, is attended with an augmented exhalation of carbonic acid, and, as will be afterwards seen, with an increased

development of animal heat. Of course there must be limits to this result.

MM. Andral and Gavarret have arrived at some remarkable results regarding the influence of *sex and age* on the exhalation of carbonic acid. They found that after the age of eight years, the male exhales much more than the female, the average quantity between the ages of 16 and 40 being double in the male. With respect to each sex at different ages, the male child between 8 and 15 exhales *per hour*, in the form of carbonic acid gas, 77 grains of carbon; the female about 15 grains less. In the *male*, the quantity increases rather suddenly at puberty to 157 grains, and continues increasing up to 25, when it averages 191 grains per hour (or 9½ ounces per day). It remains about stationary up to 40 years of age; between 40 and 60, it averages only 155 grains; and between 60 and 80, 141 grains per hour. In one man of 102, remarkably hale, it was only 91 grains; in another of 26, remarkably fine and muscular, it reached 217 grains. In the *female*, no great or corresponding increase takes place at puberty; and as long as menstruation is regular, the average exhalation of carbon is only 98 grains per hour. During pregnancy, however, and also at the period of the cessation of the menses, it is singular to observe that this quantity is quickly raised to 129 grains. Between 50 and 60, the average is 112 grains; between 60 and 80, 104 grains. In a woman of 82 it was only 92 grains per hour. Scharling has to some extent corroborated these results.

This increase in the male during the period of the greatest activity and muscular vigour, and also the general higher standard in the male, and the decline in both sexes with age, is accordant with what we know of the rate and activity of the changes of nutrition under these several conditions. The varieties in the female are less easily explained, though obviously of great importance. It may be here remarked, that Hutchinson and Bourgery have ascertained that the quantity of *air breathed* increases up to 30 or 35 years of age, then decreases slowly to 65, and very much in old age; and also that it is less in females.

Such are some natural circumstances modifying the quantity of carbonic acid exhaled. The following conclusions of Vierordt on the *influence of the respiratory movements* on the amount expired are interesting in themselves, and throw light on the theory of the respiratory function. He finds, that when the respirations are increased in frequency, more carbonic acid is exhaled, although from the much larger quantity of air breathed, the per centage of

carbonic acid in the expired air is less. Thus the per centage of this gas bears a certain proportion to the frequency of the respirations, supposing their bulk to remain the same.

If the respiratory movements are suspended for a short time, the per centage of carbonic acid in the expired air becomes increased. The total quantity expired is, on the other hand, somewhat diminished; showing that this increased per centage, in a given quantity of air, does not compensate for the smaller proportion of air entering the lungs under these circumstances.

Allen and Pepys found, that when the same air was breathed more than once, the proportion of carbonic acid underwent a considerable increase. Air breathed nine or ten times, contained 9·5 per cent. of carbonic acid; but if the air was breathed over again as often as possible, the per centage of this gas could not be increased above 10. Mr. Coathupe obtained as much as 12·75 per cent. of carbonic acid from air in which animals had been placed until they were suffocated.

The per centage of carbonic acid varies also at different periods of time during the same respiration. By taking the average of twenty-one experiments, Vierordt found, that while the proportion of carbonic acid in the entire expiration amounted to 4·48 per cent., the first half contained 3·72, and the last half 5·44 per cent. It has been estimated, that the air from the air-cells contains as much as 5·83 per cent. of carbonic acid, or about 1·3 per cent. more than the air of an ordinary expiration.

Amount of Oxygen Inhaled.—The quantity of oxygen introduced into the system in respiration, is always greater than is required to form the amount of carbonic acid eliminated during this process. This surplus quantity no doubt is employed in oxydizing other substances in the organism besides the carbon; such, for instance, as sulphur and phosphorus, which are eliminated in the urine in the form of sulphuric and phosphoric acids. Valentin and Brunner found that the proportions of these gases approximated very closely to their diffusive volumes; for the quantities obtained by direct experiment, and by calculation, differed very slightly. Oxygen being the lighter gas, a larger quantity is required to replace the carbonic acid; 81 parts of the latter will require 95 of the former to replace it according to Graham's law, that the diffusion volume of different gases varies inversely as the square root of the density, or about one volume of absorbed oxygen corresponds to ·85 of exhaled carbonic acid. The experiments of Dulong and Despretz,

as well as those of Regnault and Reiset, have, however, shown that this relation is by no means constant.

From the above considerations, it is evident, that the respiratory changes cannot be efficiently carried on, unless a certain proportion of air be assigned to each individual living in a confined space. For if the cubic capacity of the apartment be below a certain standard, the air becomes so contaminated by the increased quantity of carbonic acid expired, as to produce a highly deleterious effect upon the health.

Probably between four and five hundred cubic feet of air pass through the lungs daily, and in the same period, about twenty-three cubic feet of oxygen gas are absorbed. The size of an apartment, therefore, in which persons are confined should be such, and its ventilation should be so arranged, that each individual may be supplied with the above quantity of pure air as a minimum. The cubic capacity of such rooms should not be less than 800 cubic feet for each person inhabiting them. Leblanc found, that in the Chamber of Deputies in Paris, each individual was supplied with only from 353 to 706 cubic feet of air per hour; and in the air issuing from the apartment, he found from 2 to 4 of carbonic acid in 1000 parts by weight. This proportion of fresh air was probably too small, since it has been found that 1 per cent. of carbonic acid produces a deleterious effect upon the system when breathed for a long time continuously. In the Model Prison, Pentonville, from 1800 to 2700 cubic feet of fresh air pass into each cell per hour. In hospitals, the number of patients in each ward should be so arranged, that not less than from 800 to 1000 cubic feet should be assigned to each. In the new King's College Hospital, each patient has from 1850 to 2500 cubic feet of air.

Dr. Snow has shown that the bad effects of air deteriorated by respiration, are due not only to the increased quantity of carbonic acid which it contains, but also to the diminution of its oxygen. From his experiments upon animals he has been led to conclude, "that 5 or 6 per cent. by volume of carbonic acid cannot exist in the air without danger to life, and that less than half this amount will soon be fatal, when it is formed at the expense of the oxygen of the air."

Exhalation of Nitrogen.—MM. Regnault and Reiset have shown that an extremely small quantity of nitrogen is constantly exhaled, its proportion varying according to the nature of the food. After prolonged fasting, this gas, however, appears to be absorbed, instead of being exhaled. Barral found that the quantity of nitrogen

exhaled from the lungs of man, was about $\frac{1}{100}$th of the amount of carbonic acid removed in the same time. It must also be observed, that a very small proportion of nitrogen is constantly being expired in the form of ammonia.

Changes in the Blood resulting from Respiration.—Dark venous blood in its passage through the capillary vessels of the lungs assumes the bright red colour characteristic of arterial blood. This change, as is well known, depends upon the removal of carbonic acid gas and the absorption of oxygen. Magnus showed that venous blood contained 25 per cent. of its volume of carbonic acid, and 5 per cent. of oxygen; and that arterial blood, on the other hand, contained as much as 10 per cent. of its volume of oxygen, and only 20 per cent. of carbonic acid. The seat of this change is clearly in the red blood corpuscles; but its precise nature has not yet been satisfactorily determined. It has been ascribed to a chemical change taking place in the coloured constituent of the blood globule (page 304), but later researches render it probable that it is, at least in some measure, due to a physical alteration. Henle was the first observer who referred the change of colour in the blood corpuscle to a change in its form.

Scherer states that the blood corpuscles of venous blood are nearly spherical, and their walls thin and transparent, a condition which causes them to transmit light freely. On the other hand, the corpuscles of arterial blood are bi-concave, their walls thicker, and they reflect light more readily, which is considered to account for the brighter colour of arterial blood. Harless has even been able to measure the difference in size between the blood corpuscles of arterial and venous blood of the frog.

Magnus proved that serum would dissolve twice as much carbonic acid as an equal quantity of pure water, a power which Liebig attributed to the amount of phosphate of soda contained in blood serum.

Of the gases existing in the blood, a very small proportion only is in chemical combination with any of the constituents of that fluid, but the greater quantity is held in solution in a free and uncombined state. This is readily proved by passing a current of hydrogen gas through some defibrinated blood placed in a bottle to which tubes are adapted. The hydrogen takes the place of the gases previously held in solution and the latter escape; and by causing them to pass through lime-water, evidence of the presence of much carbonic acid is at once obtained by the formation of a precipitate of carbonate of lime. If the carbonic acid had existed

in a state of chemical combination, we should not have been able to obtain evidence of its presence by this process. Besides much carbonic acid, oxygen, and a little nitrogen, are held in solution in blood.

With reference to the oxygen, it cannot be doubted that part is in chemical combination with the constituents of the blood corpuscle, and part in a state of simple solution.

The chief agents in effecting the absorption of gases in the blood are undoubtedly the blood corpuscles, for it has been clearly proved by Davy and others, that defibrinated blood possesses the power of absorbing gases in a greater degree than blood serum. Magnus found that blood was capable of absorbing $1\frac{1}{2}$ times its volume of carbonic acid gas.

From the researches of Professor Lehmann upon the crystallizable contents of the blood corpuscle, originally discovered by Otto Funke, we are led to conclude that the colouring matter of the blood is chemically affected by oxygen and carbonic acid gases.

Lehmann has shown, that if oxygen is allowed to pass through defibrinated blood slowly for fifteen minutes, and is followed by the transmission of a current of carbonic acid for five minutes under the influence of light, these crystals are formed in larger quantity, and more rapidly, than if the carbonic acid is passed through the blood first. These crystals are composed of a definite chemical compound; and there can be little doubt that the influence which the gases exert upon its crystallizing properties are of a chemical nature.*

It was formerly supposed that the oxygen of the air combined with the carbon of the venous blood in the pulmonary capillaries, and that the carbonic acid eliminated from the system was formed at the pulmonary surface; but later researches have shown, that this gas exists pre-formed in the blood, and is therefore only *exhaled* from the fluid contained in the vessels of the lungs, a view which was first advocated by Lagrange and Hassenfratz in 1791. It has been found that animals will give up carbonic acid when placed in atmospheres which do not contain any oxygen, a fact which could not be accounted for upon the supposition that this gas was formed by the combination taking place in the pulmonary organ. Again, the presence of both free oxygen and carbonic acid

* For much interesting matter upon the subject of blood-crystallization, the reader is referred to Lehmann's "Physiological Chemistry," 1853, translated by Dr. Day, Cavendish Society, vol. iii.

can be proved in the arterial and venous blood. Moreover, blood may be caused to absorb, or to give up, these gases after it has been removed from the body.

All the tissues of the body contain a small quantity of dissolved gases; and carbonic acid can be detected in all the animal fluids, even in the urine.

Frogs' muscles, carefully deprived of nerves and vessels, will give out carbonic acid if placed in an atmosphere of oxygen gas, and it has been shown by G. Liebig, that the muscles continue to absorb oxygen, and to exhale carbonic acid, as long as their power of contractility lasts, and that they retain their contractile power for a much longer period in an atmosphere of oxygen gas than in one of hydrogen, nitrogen, etc. The careful observations of Lehmann upon the respiration of insects (in which class the air is directly carried to the elements of the tissues by the tracheæ), tend still further to prove the truth of this view. We may therefore conclude, that the oxygen of the air is carried by the blood to the ultimate elements of the tissues, and that here chemical combination takes place and carbonic acid is produced; the carbonic acid being then transmitted to the lungs in solution in the venous blood, and there exhaled.

Quantity of Carbon removed from the Body.—The estimation of the amount of carbon eliminated from the organism in a given time is a matter of great difficulty, and the results of the experiments of observers present wide differences. Allen and Pepys calculated the daily quantity at rather more than 11 oz. troy, while Mr. Coathupe estimated it at only 4·97 ounces, and Scharling at 7·382 ounces.

The method employed by Liebig consisted in subtracting the total quantity of carbon in the fæces and urine from that present in the food; the remainder represented the quantity excreted in the breath in the form of carbonic acid. From these data, Liebig calculates that an adult male, taking moderate exercise, loses 13·9 ounces of carbon daily from the lungs and skin. In order to convert this large quantity of carbon into carbonic acid, 37 ounces of oxygen must be absorbed during the same period by the lungs and skin; but this estimate is doubtless too high. Andral and Gavarret estimated the carbon at nine ounces.

According to the recent accurate investigations of Scharling, a powerful adult man exhales in the course of twenty-four hours about 30·6 oz. of carbonic acid, which corresponds to 8·34 oz. of carbon, and this we may look upon as a correct estimate.

Some very accurate experiments upon this subject have been made by M. Barral upon himself during summer and winter. The great difference noticed in the quantity of carbon exhaled at different periods of the year may, to some extent, explain the discrepancies in the results of various observers—

	Weight of body.	Carbon in food.	Carbon excreted. In fæces.	In Urine.	Exhaled.
	lbs.	grs.	grs.	grs.	grs.
In Summer.....	104·5	5654·1	236·2	234·6	5183·3
In Winter......	„	4090·0	137·4	211·5	3741·1

About 10·8 oz. troy of carbon, therefore, passed off daily in the form of carbonic acid in winter, and 7·8 oz. in summer. The amount of carbon eliminated by respiration will also be influenced by the quantity and nature of the food, and by other circumstances, which have been previously adverted to.

Theory of Respiration.—By the interchange of gases in the lungs, the venous blood becomes of the bright scarlet colour characteristic of arterial blood. The oxygen and carbonic acid both permeate the delicate, moist, limitary membrane of the air-cells at the same time, but in opposite directions.

The oxygen, having passed through the capillary walls, is held in solution in the blood; a small part entering into chemical combination with the contents of the blood corpuscle, and to a less degree with some of the constituents of the serum.

A portion of the oxygen not improbably acts directly upon certain substances contained in the circulating blood, and contributes to the formation of carbonic acid. In this way some of the elements of the food lately introduced into the blood may become decomposed, and their carbon removed in the form of carbonic acid. The greater portion of the oxygen is no doubt carried to the capillaries, and much of it then leaving the blood, and passing through the capillary walls, becomes dissolved by the intercellular fluid, in obedience to the same physical laws by which it was absorbed. At the same time, the carbonic acid formed in the interstices of the tissues, and dissolved by the fluid which moistens their ultimate elements, leaves this latter to enter the blood, from which the oxygen has just been removed, and causes it to assume the colour of venous blood.

Here, then, are two sources of carbonic acid—one resulting from the action of the oxygen upon certain elements recently introduced in the food, giving rise to the production of a certain amount of

animal heat, and the other depending upon the union of the oxygen with the carbon of those substances which are produced in the disintegration of tissues during the performance of their functions; in this combination also heat is developed.

In purely carnivorous animals, the greater portion of the carbonic acid results from the disintegration of the muscular and nervous tissues; while, in the herbivora, much of the food, rich in carbon and poor in nitrogen, is at once converted into carbonic acid.

Although the action of the oxygen upon the carbon of the compounds, from which the carbonic acid is formed, is a strictly chemical process, the application of this oxygen to the substance to be decomposed, and the removal of the resulting carbonic acid, are dependent solely upon the physical relations which these gases bear to each other, to the membrane through which they pass, and to the fluids in which they are dissolved.

The blood, loaded with carbonic acid, at length returns to the respiratory surface, where it parts with this gas and absorbs oxygen, in obedience to the physical laws above referred to.

More oxygen is usually absorbed than is necessary to convert the carbon into carbonic acid. This is required for the oxidation of other elements, as sulphur and phosphorus, by which compounds are produced which are eliminated by other emunctories.

The amount of oxygen inhaled will depend in great measure upon the quantity and nature of the food, and upon the activity of the vital functions, and is intimately associated with the production of animal heat, as will appear in the next chapter.

It has been shown that the activity of the respiratory function is materially influenced by various external and internal conditions. Temperature, a dry or moist state of the atmosphere, the period of the day, the digestive process, rest, exercise, etc., all exert an influence on the amount of oxygen inhaled and of carbonic acid exhaled. These are points which must be borne in mind by the careful practitioner in the treatment of such diseases as phthisis, pneumonia, emphysema, and the like.

Respiration is, therefore, partly a physical and partly a chemical process;—chemical, as far as regards the results; physical, with reference to the means by which these results are produced. The introduction of the restorative oxygen, and the removal of the deleterious carbonic acid, are effected solely by a physical process; while the formation of the carbonic acid is essentially a chemical process, and in its production many complicated chemical decompositions take place.

The great objects of respiration are, first, the introduction of oxygen, by which the products resulting from the disintegration of tissues are converted into compounds, which are easily eliminated from the body by the different organs of secretion; and secondly, the removal of the most important and most destructive of these, carbonic acid, at the pulmonary surface.*

* Upon the subjects discussed in the present chapter, reference may be made to the following works:—Article "Respiration," by Dr. John Reid, Cyclopædia of Anatomy and Physiology; "Thorax," by Dr. Hutchinson; Physiological, Anatomical, and Pathological Researches, by Dr. John Reid; Recherches sur la Structure intime du Poumon. Rossignol, Bruxelles, 1846. The following systematic works—Müller's Physiology; Bostock's System of Physiology; Principles of Human Physiology, by Dr. Carpenter.

On the Mechanism of Respiration.—Dr. Sibson, Phil. Trans. 1846; Med. Chir. Trans., vol. xxxi.; Dr. Hutchinson, Med. Chir. Trans., vol. xxix.

On the Chemistry of Respiration.—M. Barral, Ann. de Chim. et Phys., tom. xxv.; Messrs. Regnault and Reiset, Annales de Chimie et de Physique, 1849; Comptes Rendues, 1846; Lehmann's Physiological Chemistry, translated by Dr. Day, Cavendish Society, 1851—4.

CHAPTER XXX.

ON ANIMAL HEAT.—DEVELOPMENT OF HEAT IN PLANTS.—DEVELOPMENT OF HEAT IN ANIMALS.—TEMPERATURE OF THE HUMAN BODY.—INFLUENCE OF EXERCISE, SLEEP, AGE, CLIMATE AND SEASONS, FOOD AND DISEASE UPON THE DEVELOPMENT OF HEAT.—HYBERNATION.—THEORY OF ANIMAL HEAT.—INFLUENCE OF THE NERVOUS SYSTEM.—BERNARD'S RESEARCHES.

The chemical changes which are continually taking place in animals and, at least under some circumstances, in plants, are accompanied with the development of a certain amount of heat. The elevation of temperature may be so slight as to elude the ordinary means of observation; and although the sensible temperature of the organised body is very slightly higher than that of the medium in which it is placed, the quantity of heat set free in a given time may be considerable. This development of heat seems to result from the action of the oxygen upon the combustible elements of the food, and in a less degree upon those of the tissues. The chemical combination in which the largest amount of heat is disengaged in the higher animals, and upon which their high temperature seems to depend, is that of carbon and oxygen, resulting in the production of carbonic acid.

Whenever oxygen combines with carbon, hydrogen, phosphorus, sulphur, etc., or with a metal, heat is developed in an amount exactly proportioned to the quantity of substance consumed. The sensible temperature produced varies, however, with the intensity and rapidity of the chemical action. When the action is intense, the temperature rises very rapidly, and may reach a very high degree for a short time. If, on the other hand, the action is slow, the temperature may be scarcely elevated above that of the surrounding medium; but this slight elevation may continue for a considerable time. The *quantity* of heat developed in the two cases, however, is precisely the same.

Development of Heat in Plants.—Heat is developed by the seeds of plants during germination; and at the same time oxygen is removed from the air, and carbonic acid evolved. Buds, flowers and ripening fruits also evolve a certain quantity of heat.

M. Hubert, in the Isle of France, encircled a thermometer with twelve spikes of the *arum cordifolium*, and found it rise to 121° F., the temperature of the external air being 66°. During the process of flowering, the spathe of the *arum maculatum* consumed in 24 hours five times its volume of oxygen derived from the surrounding atmosphere, the termination of the spadix 30 times, and the sexual apparatus 132 times its volume, in the same period. In these experiments it was found, that if the plant was protected from the influence of the surrounding air, the development of heat ceased. In the germination of seeds, the starch is converted into gum or dextrine, and ultimately into sugar. The sugar then disappears, while oxygen is absorbed from the air, and carbonic acid evolved. The temperature at the same time rises.

In these examples, the disappearance of the starch and saccharine matters from the plant, the absorption of oxygen, the formation of carbonic acid, and the development of heat are all manifestly connected. A corresponding series of phenomena attends the development of heat in animals.

Development of Heat in Animals.—It is to be observed in the first place, that as all animals give out carbonic acid in their respiration, so all develope heat, whether they are called *cold-blooded* (reptiles and all below them), or *warm-blooded* (mammalia and birds). The cold-blooded animals are those which develope so little heat, form and give out so little carbonic acid, that they are unable to maintain a temperature much removed from that of the medium in which they live; and their circulatory and breathing organs are entirely accordant with this feeble calorifacient power. Dr. John Davy, who has made a number of valuable and exact observations on this subject, found that when the average temperature around was 79·7° F., that of reptiles was only 82°, and that of fishes nearly the same. In the case of insects, crustacea, and mollusca, there is even a closer correspondence with the temperature of the circumambient medium. Insects, however, especially when housed in communities, so that their heat is not rapidly dissipated, have shown a rise of 20° F. above the outward air—provided they were in a state of active movement. On this point, the observations of Mr. Newport are very valuable. On the other hand, warm-blooded animals (birds and mammalia), are those in which nutrition with all its attendant accessory functions, assimilation, circulation, respiration, the supply of food, and of oxygen, the formation and disengagement of carbonic acid are most active and energetic. These have a nearly uniform temperature within the limits of 96°

and 111° F., the mammalia having the lower and birds the higher, in strict accordance with the above-mentioned circumstances. A bird, for its weight, consumes much more oxygen, and sets free much more carbonic acid, while it maintains in the same medium a higher temperature, than a mammal. Finally, some degree of warmth is evolved by the egg in its development during incubation. In this process, oxygen is absorbed, and carbonic acid exhaled through the calcareous envelope.

The amount of heat developed in the animal organism, depends very much upon the nature and quantity of the food. The carbon of the food in its slowly effected union with oxygen within the organism, gives out probably as much heat as if the same quantity were burnt in oxygen gas. The development of animal heat will, therefore, in great measure depend upon the activity of the functions of respiration and circulation.

The greater part of the oxygen which an adult consumes in the twenty-four hours, instead of remaining in the body, thereby increasing its weight, unites with carbon and hydrogen, and is removed in the form of carbonic acid and water. The remainder enters into combination with other elements, and compounds are formed which are removed by the excreting glands. In these combinations a large amount of heat is developed, ranging in amount according to the conditions before referred to.

Temperature of the Human Body.—The heat of the interior of the body at those parts which are most accessible to our instruments of measurement, as, for instance in the axilla, within the mouth or rectum, is found to be about 97° or 99° F.; more frequently the latter. The temperature is, however, liable to variation according to circumstances, which modify the amount of heat generated within the body or the rapidity of its loss. Independently of this, however, great differences have been found to exist in the temperature of different parts, according to the rate of their cooling, their vascularity, distance from the centre of circulation, etc. A good idea of this will be derived from the following Table of Dr. Edwards. He examined a strong man, at rest, in July, the air being at 71° F., and found

Mouth and rectum . . .	102°
Hands	99°·5
Axillæ and groin	99°
Cheeks	96°
Feet	96°
Skin of Epigastrium . . .	95°

The best experiments on the temperature of internal parts, are those of MM. Becquerel and Breschet, who employed a thermo-electric apparatus, consisting of two wires of different metals, soldered together, and having their free ends brought into communication with an excellent thermo-electric multiplier, with an index to show 10ths of a degree. The wire, passed through various parts of the body, indicated the temperature of the tissues in contact with the point of contact of the two metals. Passing this $1\frac{1}{2}$ inch into the calf of the leg, the temperature was found to be 98° F., while at a depth of $\frac{1}{3}$ inch it was only 94°, showing the cooling from the surface inwards. The superficial fascia over the biceps was nearly 3° lower than the muscle itself; on compressing the brachial artery, so as to intercept the flow of blood, the temperature *immediately* fell several 10ths of a degree. So after the ligature of the main artery for aneurism, the temperature is well known to fall, and to require to be economised with increased clothing. Professor Fük obtained the following results in twelve experiments upon living dogs. No difference in the temperature was observed between the right and left ventricle of the heart. The highest degree of warmth was always met with in the vagina and rectum (101·75 to 105·79).

As *exercise* is attended with quickened circulation, more active respiration, a more abundant interchange of oxygen and carbonic acid, so it occasions an augmentation of animal temperature. The secretions are more copious—there is a more energetic nutrition—the quantity of food required is greater, and we all know how much more keen our appetites are, and how much more food we consume when engaged in employments requiring active exercise, than in sedentary occupations. MM. Becquerel and Breschet have observed, that the muscles during their contraction become hotter by 2° or 3°, a fact which one of us can attest from an experiment on the biceps in his own person, made by these gentlemen themselves.

Sleep, as it is attended with diminished frequency of respiration and pulse, and a smaller evolution of carbonic acid, is also marked by a slight fall of temperature, viz., of from 1° to 3° F.

Age has been shown by Dr. Edwards to have much influence on temperature. Old persons, and very young ones, are alike unable to preserve their proper warmth without external aid, and have not the same power as adults of generating heat. For example, he found that young carnivorous and rodent animals, when placed in an atmosphere of 50° F. apart from the body of the mother quickly became cold, though when lying near her they continued within 2° or 3° of her temperature. So, young sparrows one week old were at 97° F. in

the nest, but when removed from the nest, fell in one hour to 66° F., when the external air was at 62° F.; and he showed that this result was not to be attributed to their unfledged state.

Young animals, therefore, require the aid of external warmth, or at least of every means of retaining their own warmth. The nests of birds not only serve to retain the warmth of the parent during incubation, but also that of the young brood during their tender age. The human infant stands no less in need of extraneous warmth—and it may be safely affirmed, that much of the immense mortality of our infant population is owing to the want of artificial heat.

We must refer to what has been already said in the chapter on food (Chapter XXII.), for observations on the relation of the kind of food to the animal temperature.

Influence of Climate and Seasons.—The best account we possess of the effect of climate results from 4000 experiments made on board the Bonite, a French vessel, during her passage between Cape Horn and the tropics. The mean temperature of 10 men at Cape Horn with the thermometer at 32° F. was hardly two degrees lower than at Calcutta, where the thermometer stood at 104° F. The temperature of the body was found to rise and fall perceptibly, but slightly—to fall slowly in passing from a warm to a cold climate, and to rise more rapidly in re-entering the torrid zone.

The rate at which an animal loses its heat will depend both on the coldness of the surrounding air, and on the rapidity of evaporation. In temperate climates these causes differ inversely with the season. In winter there is much loss by radiation, little by evaporation, in summer the reverse. But Dr. Edwards has well shown that these compensations are not the only cause of the uniformity of temperature so wonderfully maintained, but that there is also in animals a difference in the rate at which heat is produced, according to the season, "the calorific faculty is more active in winter than in summer." "In winter there is a more active production with greater loss, in summer a less production with smaller loss." To test this, Dr. Edwards contrived a box, surrounded with ice, having the same external temperature and the same humidity of atmosphere in winter and summer, so that the loss by radiation and evaporation should be the same in both cases. Into this apparatus, in February, he placed 5 sparrows that had been living in a warm room, and found that after an interval of 3 hours they maintained their previous heat within 1° F. Again, in July, he did the same with 4 others, and these after 3 hours were found to

have lost 10° F. We may here recall the fact, that the quantity of carbonic acid exhaled is greater when the external temperature is low. Mice and guinea-pigs evolve twice as much carbonic acid at 32° as at 60° F., and birds more than double. Also more food, and of the calorifacient kind, is required in winter than in summer, and in cold climates than in warm.

The nature of the food must vary with the temperature of the climate, for at the same time that the respirations are less in number in hot than in cold climates, the air is less dense, and contains in a given volume less oxygen; hence a light and succulent diet is better adapted to the requirements of the system, and comparatively little heat is developed; while, in cold climates, a large quantity of highly carbonaceous food is necessary in order to furnish the requisite supply of heat.

In animals which are very active, and which are not subjected to the cooling influence of an atmosphere many degrees lower in temperature than their own bodies, it is quite possible that a sufficient amount of heat may be generated in the combination of the elements of their tissues without the necessity of fatty or starchy food forming a part of their highly nitrogenous diet. In cold climates, however, a large quantity of readily combustible food is necessary in order to furnish the requisite amount of heat.

Loss of Heat by Evaporation.—The animal body is continually subject to evaporation of its fluid parts, just as any other moist substance, and the amount of evaporation, and the consequent loss of heat, will depend on the same causes as in the case of inorganic substances. The moisture, or dryness, of the surrounding air, and its state of motion or rest will mainly influence the result. All the effects of excessive temperature on the body are much more apparent with a moist than a dry atmosphere; because in the case of a dry atmosphere a greater amount of evaporation takes place, and hence a greater quantity of heat is removed from the system.

In England it would be impossible to sustain a vapour bath at a temperature of 110° or 120° for more than 10 minutes, whereas the body may be without danger exposed for the same time to a dry temperature twice as high or more. In some well-known experiments Sir Charles Blagden remained immersed for 8 minutes in dry air heated to the extraordinary pitch of 240° or 260° F. An oppressive day in summer is one where the air is moist at the same time that it is hot and stagnant.

Again, the refrigeration, arising from simple contact of cold air,

is much increased by motion of the air, *i. e.*, by a rapid renewal of fresh cold particles; and all the more if the moving air be dry. A cold dry wind is one of the most powerful refrigerators, but we could hardly realise the full extent to which this is true, without an example. Mr. Fisher, the surgeon to the expedition to the Polar Seas under Sir Edward Parry, has related its extraordinary effects. The hardy sailors found that they could better bear a cold which would freeze mercury (viz., 40° below zero, F.) when the air was perfectly calm, than a temperature of 10° F. (*i. e.*, 50° higher) when the wind was up.

The rate of cooling, and the amount of heat parted with in this manner depends upon the difference in temperature between the body and that of the surrounding medium. The loss of heat must of course be much greater in the Polar regions, where the temperature is 100° or more below that of the body, than in hot climates where the temperature of the air approximates to that of the body. Yet the temperature of the blood is the same in each case. The cooling effects of cold climates are compensated for by the increased quantity of highly carbonaceous food taken, and the increased activity of the respiratory functions. A much larger quantity of carbonic acid is evolved, and a much greater amount of heat liberated, than in warm climates, where the food must be smaller in quantity, and should contain less carbon and hydrogen.

Warm clothing, by protecting the body from the influence of cold air, and so preventing the loss of a certain amount of heat, may be said, as Liebig has remarked, to be equivalent in cold countries to a certain amount of food. The appetite is increased in cold weather, and if in winter we clothe lightly we shall eat more than if warmly clad. We may often remark, that lean spare men, who take a great deal of exercise, consume many times the quantity of food which satisfies a moderately plump individual. The former has usually a larger respiratory capacity, and is less protected from the cooling influence of the external air.

Influence of Food.—If an insufficient quantity of food be taken, the temperature of the body falls, and the carbon and hydrogen, entering into the composition of the tissues themselves, combine with the oxygen, and thus a certain amount of heat is furnished. Deficiency of food is borne much more readily in a high temperature than in a low one. Cold very much expedites death from starvation. The highly-important and interesting experiments of Chossat* upon

* Recherches expérimentales sur l'Inanition.

animals have shown that in starvation the fatty matters, which are most readily convertible into carbonic acid, are first removed, soon afterwards the substance of the muscles is acted upon, in order to furnish an amount of heat, without the development of which life would at once cease; next the nervous system gives way to this oxydizing power,—life ceases, and every portion of the organic material, with the exception of the mineral matters combined with it, is brought under the destructive influence of the oxygen. M. Chossat found that, taking 40 per cent. as the mean, fat lost 93·3, blood 75, heart 44·8, muscles 42·3, skin 33·3, bones 16·7, and the nervous system only 1·9 per cent. of their weight in fatal starvation.

The time required to produce death from starvation varies according to different circumstances. If the body be very fat, life will be supported for a longer period than if only a small quantity of fatty material be present. A fat pig, which was confined by a slip of earth, lived 160 days without food, and during this period he lost more than 120 lbs. (Martell Trans. Linn. Soc., vol. xi. p. 411, quoted in Liebig's letters). While death from starvation would be retarded by warmth, little or no exercise, and a moderate supply of water, it would be much accelerated by the converse of these circumstances.

Influence of Disease.—In acute diseases accompanied with fever, such as pneumonia, pleurisy, acute rheumatism, and in scarlatina, typhoid fever, etc., the temperature often rises several degrees above the normal standard, not unfrequently reaching 105° or 106° F. Dr. Edwards observed the temperature as high as 110¾ in a case of tetanus. This high temperature sometimes decreases rapidly, and sometimes very gradually, the diminution being frequently accompanied by free perspiration and copious excretion of urine, rich in urea and lithates. The frequency of the pulse also diminishes at the same time. This increased development of heat, during the exacerbation of the fever, is associated with the increased amount of disintegration of tissues taking place at that time; while the remission is accompanied by the elimination of the resulting compounds, free perspiration, diminished frequency of pulse, and corresponding decrease of temperature.*

In those diseases, on the other hand, where the activity of the chemical processes going on in the body is impaired, the temperature falls many degrees below the normal standard. In cholera, where the dark blood and imperfect respiration mark the introduction of an

* See a review, by Dr. H. Weber, in the *Medico-Chir. Review*, Jan. 1853, on Crises and Critical Days, by Dr. L. Traube. Berlin, 1852.

inefficient supply of oxygen, and the suspension of secretion and the absence of symptoms characteristic of the accumulation of excretory products in the organism, show that the chemical changes accompanying the disintegration of the tissues are only taking place in a slight degree, or are altogether suspended, the temperature often falls to 70°, or even much lower. It is curious that, in many of these conditions, the temperature should rise very rapidly immediately after death. The most striking examples of this have been placed on record by Dr. B. Dowler, of New Orleans, and occurred in cases of yellow fever, etc. In one instance, just before death, the temperature was 104°; and fifteen minutes after death, it had risen to 113° in an incision in the thigh. The temperature still remained very high for several hours after death.

Hybernation.—The phenomena of hybernation are dependent upon the conditions we have just alluded to. Previous to becoming torpid, the animal accumulates a quantity of fat, which is, as it were, laid up as in a storehouse, to be consumed slowly, while the period of annual sleep lasts. At this time, the activity of the vital functions is much reduced, the animal lies perfectly still, the frequency of the heart's action and of the respirations diminishes; its temperature falls many degrees, and it is placed in a condition the most favourable for supporting life for a considerable period of time with a very small supply of combustible material. The moment the animal is roused, the vital processes again become active, and a supply of food soon becomes necessary. In the case of the marmot, in which animal the hybernation is complete, the pulse falls to about 15 beats in a minute, and the respirations to 14 in an hour, while in the waking state these are respectively 150 and 500. The temperature of the body, during the hybernating period, may fall as low as 35°. If, however, the animal be exposed to warmth, the frequency of the pulse and respiration increases, a much larger quantity of oxygen is consumed, and a corresponding proportion of carbonic acid exhaled. The temperature of the body suddenly rises, and the animal soon dies, unless supplied with food.

Theory of Animal Heat.—It has been shown, that in certain parts of *plants*, and in cold as well as warm-blooded *animals*, heat is developed coincidently with the consumption of oxygen, the combustion of carbon, and the formation of carbonic acid. The heat produced, and the chemical product of combustion, have been observed to bear a certain general correspondence one with the other.

To understand the real nature of the development of heat in

organized bodies, it is necessary to remember, that the heat disengaged during the oxidation of carbon or of a metal (i. e. during the combustion of these bodies) is directly proportioned to the amount and not to the intensity of the chemical action. In the words of a distinguished chemist, "The rod of iron that is burnt in oxygen gas, produces a heat which no one will deny; but the iron which rusts slowly in the air, disengages just as much heat, although its temperature never rises sensibly above that of the surrounding atmosphere. Phosphorus alight burns brilliantly, and produces abundance of heat; phosphorus in the cold, still burns, but with little lustre, and the heat which it evolves was for a long time denied."*

It has been already stated (p. 152-4) that a large portion of the food being destitute of nitrogen, is not the best adapted to form part of the tissues of the body into the composition of which that element enters. This *calorifacient* food (consisting of various quantities of carbon in combination with oxygen and hydrogen, in the proportion in which these last form water, as starch, sugar, cellulose, or gum, or of carbon and hydrogen in combination with a less proportion of oxygen in fatty matters) seems to be devoted in the main to the production of heat by the combination of its carbon and hydrogen with the oxygen furnished by respiration. It is a question through what changes it passes ere thus consumed; but of its eventual destination to the production of heat there would appear to be no doubt.

As was shown in the chapter on Respiration, more oxygen is taken into the blood by the lungs than is required to form the carbonic acid exhaled. This superfluous oxygen disappears, the greater part appearing to enter into combination with hydrogen, while a small quantity goes to oxidize the sulphur and phosphorus. The air breathed is likewise found to have lost bulk. Now gaseous carbonic acid contains its own bulk of oxygen—but oxygen uniting with hydrogen to form water is condensed. Such a condensation of the oxygen would accord with the observed diminution of bulk in air by being respired. It has been remarked that herbivorous animals return to the air, as carbonic acid, only nine out of ten of the volumes of oxygen absorbed in respiration, and that carnivorous animals return in the same form, only five or six out of ten volumes. The carnivora, then, absorb nearly twice as much oxygen as they employ for oxidizing carbon, and a very large proportion of the remainder, no doubt, combines with hydrogen to form water.

* Dumas, "Balance of Organic Nature," p. 37.

To explain the prompt oxidation of the carbon and hydrogen within the body, Liebig has pointed out that the oxygen is presented to them not in a gaseous but in a liquid or solid form—that in the innumerable channels of the circulation, these several elements are not merely brought together in a very subdivided state, but everywhere in close proximity to membranous surfaces, mechanically adapted to favour the occurrence of chemical union. Moreover, that the carbon and hydrogen are not offered to the oxygen in their pure and simple state, but in combinations already existing and ready to be dissolved. He also insists, with great force, on the analogy of these actions to those promoted by the presence of a body already undergoing oxidation. For example, "when weak brandy is allowed to trickle over shavings in a closed vessel, through which a feeble current of air at from 93° to 97° F. circulates, the alcohol in the brandy remains unchanged; in spite of the greatly increased surface, no oxidation, no formation of acetic acid takes place. But if to the brandy there be added one hundred thousandth part of vinegar, beer, or wine, in the state of acetification, that is, of oxidation, the alcohol disappears with great rapidity, and is converted, by the absorption of oxygen, into an equivalent quantity of acetic acid. In the vessel, the surface of the shavings themselves very soon passes into the state of oxidation, and from this period forth, the brandy is acetified without the addition of a ferment: the wood, being in the state of decay, *eremacausis*, or slow combustion, plays the part of a ferment. These vinegar-producing vats give an idea, if only a rough one, of the process of oxidation going on in the animal body. As in the body, so also in these vessels, a temperature higher than that of the surrounding media is kept up, without the aid of external heat."*

These actions of *contact* or *catalysis* may well be supposed to play a large and most important part, not merely in the production of animal heat, but also in all the chemical changes which are ever going on in the body, from the first reception of food to the final expulsion of its elements in other forms of combination. Great obscurity, however, still hangs over the series of transformations which the food undergoes in its passage through the body.

It has been seen that both arterial and venous blood contain oxygen and carbonic acid gas in a state of solution; but into what form of combination the oxygen first enters, or from what immediate source the carbonic acid is derived is as yet matter of con-

* "Animal Chemistry," p. 34, 3rd edition, Part I.

jecture only. It may be regarded as most probable that the chemical changes which issue in the formation of carbonic acid and water, and the disengagement of heat, are effected in the tissues themselves, or in the systemic capillaries, in the immediate vicinity of the tissues.

Influence of the Nervous System.—Much difference of opinion has existed as to the share taken by the nervous system in the production and maintenance of animal temperature, some distinguished men having argued that this system is in some way the source of heat, while others have limited its operation to the exercise of a controlling and regulating influence over this important function. The latter conclusion is that to which a just estimate of the numerous facts advanced on both sides would appear to lead. The experiments of Dulong, repeated and modified by Despretz, seemed, indeed, for some time to indicate that a portion of the heat developed in the body could not be referred to the consumption of the oxygen inhaled, and that, therefore, some other source for it must be sought. They compared the heat given to a calorimeter by an animal placed within it, with that produced by the combustion out of the body of as much carbon and hydrogen as the animal gave off in the same time, in the form of carbonic acid and water, and found that more heat was given off by the animal than the chemical products of its respiration would account for, to the extent of from one-fifth to one-tenth. It has since been shown, however, that, on the one hand, allowance was not made for an actual cooling down of the animal below its normal temperature by exposure to the refrigerating influence of the calorimeter, so that the heat indicated had not all been produced within the period of the experiment; and, on the other, that the heat generated by the corresponding chemical actions out of the body had been under-estimated. Dulong himself furnished a more correct estimate of the heat developed by the combustion of hydrogen; and his results have been confirmed by Fabre and Silberman. Hence, while it would be premature to attach too much value to such experiments, considering our ignorance of the exact series of chemical changes indicated by the resultant carbonic acid and water, they certainly are not, as they once seemed to be, opposed to the chemical theory of animal heat.

It may be regarded as certain, that the nervous system exerts a considerable influence upon the development of heat in the body. The experiments of Sir Benjamin Brodie, and subsequently those of Le Gallois and Chossat, have established the fact that lesions

of the nervous centres are accompanied with a diminution of temperature, and of the power of forming heat. Again, the temperature of paralized limbs is almost always less than that of sound limbs, and often so to a very marked degree. In some instances, however, twin lesions of the nervous system are followed by an opposite effect. Much light has been thrown upon the influence of the nervous system upon the development of heat, by the recent highly interesting and important researches of M. Bernard.

Bernard has lately established the very interesting fact, that section of the sympathetic nerve is followed by a considerable elevation of temperature in that side of the head or face corresponding to the divided trunk. This increase of temperature occurs immediately; and persists after all increased vascularity and turgescence have disappeared, and after the wound in the neck has quite healed. The same observer found that sections of nerves of motion and sensation produce respectively, besides paralysis, a diminution of temperature, while, if a mixed nerve containing fibres of the sympathetic, as the facial, is divided, an exaltation of temperature takes place, arising, doubtless, from the division of the sympathetic fibres. The increase of temperature seems to be a special result of the division of the sympathetic.

Now, if the upper extremity of the sympathetic, which has been divided in the neck of an animal, be subjected to an interrupted galvanic current, the exalted temperature which follows its division is no longer manifested, and the parts supplied by it actually fall below the normal standard, and they rise again when the current is stopped. When an animal, in which the sympathetic had been divided, was placed under the influence of chloroform, the temperature which had risen several degrees in consequence of the division of the nerve, fell, while it again rose when the animal had recovered from the effects of the chloroform.

Bernard has shown that the increased temperature following division of the sympathetic, or removal of the superior cervical ganglion, cannot be attributed solely to the increased quantity of blood which is allowed to enter the vessels in consequence of paralysis of their contractile coats; for it occurs when the blood is allowed to stagnate in the vessels by tying them. At the same time, it is necessary that the vessels should contain blood. The enlargement of the vessels and the increased flow of blood to the parts are to be looked upon as the result of the altered nutritive changes which take place in consequence of the division of the sympathetic, rather than as the cause of the rise of temperature.

Whatever may be the exact order and nature of the changes which ensue, they may be looked upon as a more active manifestation of the ordinary phenomena of animal heat.

This increase of temperature, which is found generally to accompany the abstraction of nervous influence, has been accounted for by the supposition that the tissues were more readily acted upon by the oxygen of the air when deprived of the protective agency of the nervous system; but although this increased action of the oxygen, or more rapid combustion, may perhaps have considerable weight in the production of these phenomena, it must, by no means, be regarded as the sole cause, nor can the chemical theory of animal heat, as it at present stands, be considered as giving an explanation of the whole of the facts observed in connection with this highly interesting but abstruse subject.*

* Upon the subject of Animal Heat, the following works may be consulted:—Dr. Crawford's "Experiments and Observations on Animal Heat," 1788; Dr. J. Davy's Memoirs in the Philosophical Transactions, 1814; "Recherches Expérimentales sur l'Inanition," M. Chossat, Paris, 1843; Liebig's Animal Chemistry, 3rd edition; Sir Benjamin Brodie's Physiological Researches, and also papers in the Phil. Trans., 1811—12; the article Animal Heat, by Dr. Edwards, in the Cyclopædia of Anatomy and Physiology, vol. ii.; Lehmann's Physiological Chemistry; Mr. Newport on the Temperature of Insects, in the Phil. Trans., 1837; Mem. "Sur la Chaleur Animale," par MM. Becquerel and Breschet, in Ann. des Sciences Nat. Seconde Serie, tom. 3, 4, et 9. M. Bernard, "Recherches Expérimentales sur la Grand Sympathique," Paris, 1854.

CHAPTER XXXI.

VOICE.—HOW PRODUCED.—ITS EXISTENCE IN THE ANIMAL KINGDOM. —THE HUMAN LARYNX.—ITS CARTILAGES.—THEIR ARTICULATIONS AND LIGAMENTS.—CHORDÆ VOCALES.—MUCOUS MEMBRANE.— MUSCLES, EXTRINSIC AND INTRINSIC.—ACTION OF THE LARYNGEAL MUSCLES.—NERVES.—ACTION OF THE LARYNX.—THEORY OF VOCALIZATION.—CHEST VOICE.—FALSETTO VOICE.—SINGING.—INFLUENCE OF THE NERVES ON VOICE.—SPEECH.

The high development of man's intellect, as compared with that of the lower animals, would be of comparatively little advantage without his peculiar endowment of speech. To this power, an essential subsidiary is that of producing vocal sounds or voice; which, however, he enjoys in common with a large number of the lower classes.

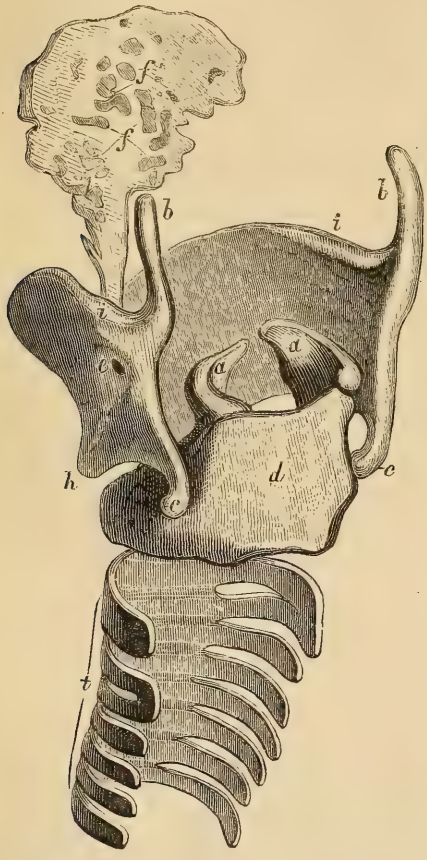
The phenomena of voice are produced by a very beautiful and simple mechanical contrivance, the larynx, which is placed at the top of the trachea, to take advantage, as an exciting force, of the air emitted from the lungs during expiration. The air thus expelled creates vibrations in certain tense and elastic membranes (*chordæ vocales*), the boundaries of a chink which is the orifice at once of entrance and of exit for the supply of air to the lungs. These vibrations generate voice.

That the larnyx is the organ of voice is proved by the following very obvious facts:—first, the least alteration in the condition of the mucous membrane covering the vocal cords is invariably accompanied by a change in the tone of the voice, *e. g.* hoarseness; secondly, ulcerative disease eating through one or both of these vocal cords destroys or greatly impairs the voice; thirdly, opening the trachea below the vocal chords, so as to divert the current of air in expiration from the larynx, will destroy voice; and fourthly, section of the inferior laryngeal nerves, by which the influence of the will is brought to bear on its muscles, and so the tension of the vocal cords is regulated, destroys the voice; lastly, by experiment on the dead larynx, sounds may be produced resembling those of

the voice. If a current of air be made to play on the vocal chords by a bellows fixed to the tracheal end of the larynx, or by blowing air through it, distinct vocal sounds are excited which can be varied by altering the tension of the vocal chords.

There is no instance of true voice among the lower orders of creation except in those animals that have a larynx connected with the respiratory apparatus as in man. In other words, all animals that have no larynx are voiceless. The hum of insects is a phenomenon essentially different from voice, and is caused by the rapid vibration of an apparatus connected with their wings. All the other invertebrated classes are incapable of producing sounds. Fishes, likewise, are voiceless. The Batrachian reptiles possess a larynx and can produce vocal sounds. The hissing of serpents is, likewise, laryngeal. But the Chelonian reptiles have no voice. In birds there are two organs placed, the one in front of the other, to which the name of larynx has been given by anatomists; of these, the lower, or that nearest the lungs, is the true vocal apparatus; the upper is merely a resonating or reciprocating cavity destined to enhance the intensity of the sounds generated in the lower. Cuvier showed that an opening between the two organs did not destroy the power of producing sounds, so long as the inferior larynx was uninjured.

Fig. 210.



Cartilages of larynx and epiglottis, and upper rings of trachea *in situ* seen from behind. From a preparation in the Anatomical Museum, King's College, by Mr. Cane.
a. arytenoid cartilages. *b.* superior cornu. *c.* inferior cornu. *d.* posterior surface of cricoid. *e.* foramen for superior laryngeal nerve. *f.* perforations of epiglottis. *i.* upper margin of thyroid. *t.* trachea. *h.* right inferior tubercle.

The *human larynx* is a kind of box, composed of pieces which may be moved on each other, and encloses the membranous bands in which the vocal vibrations are produced. These pieces, when articulated together, constitute the skeleton of the larynx. They are composed of cartilage, and form a very curious mechanism. There are five distinct pieces (two of which are symme-

trical) essential to this mechanism, and there are four smaller, accessory cartilages. The first are the cricoid and the thyroid cartilages, the epiglottis, and the arytenoid cartilages, which are symmetrical. To these may be added the cuneiform cartilages and the cornicula, which are merely sesamoid bodies destined to keep the folds of mucous membrane in proper position.

The *cricoid* cartilage is a ring, whose lower margin is parallel to, and united by fibrous membrane with, the first ring of the trachea. Its upper margin slopes from behind forwards, and from above downwards, so that the posterior surface of the cartilage is considerably deeper than the anterior, and affords two large concave surfaces for the attachment of the posterior crico-arytenoid muscles. Its upper border is connected in front with the lower margin of the alæ of the thyroid cartilage by an expansion of yellow fibrous tissue, which is particularly thick in front, called the crico-thyroid ligament, and which fills up the space called by surgical anatomists the crico-thyroid space. This space and ligament, bounded on each side by the crico-thyroid muscle, are penetrated by the trocar in the operation of laryngotomy. The posterior half of the upper border of the cricoid cartilage exhibits on each side an oval convex articular surface on which plays one of the arytenoid cartilages.

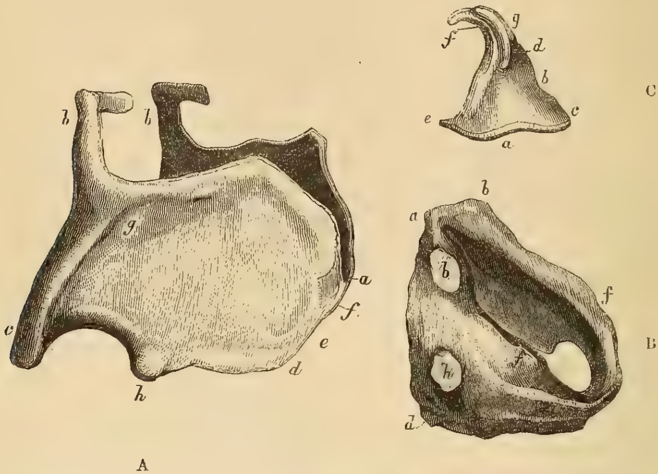
The *thyroid* cartilage consists of two square plates of cartilage (*alæ*) united at an acute angle in front; each of these is prolonged at the upper and lower corners behind, into a long superior process (*superior cornu*) and a very short inferior process (*inferior cornu*). By the superior process, and along the whole superior border of its alæ, the thyroid cartilage is united to the os hyoides by the thyro-hyoid ligament. Each inferior process rests upon the outer surface of the cricoid cartilage, and plays upon a small circular plane articular facet situated thereon.

By the angular union of the two alæ of the thyroid cartilage in front, a projection is formed beneath the integuments which is most prominent in the male, and is commonly known as the *pomum Adami*. Into the hollow angle behind, the vocal chords are inserted, and also the stalk and ligament of the epiglottis. The broad outer surfaces of the alæ, give attachment to muscles along an oblique line, which is sufficiently conspicuous between the middle and lower third of each. The thyro-hyoid and sterno-thyroid muscles are thus attached. To the inner surface of each ala are inserted the thyro-arytenoid and the crico-thyroid muscles.

By the gliding of the inferior horns of the thyroid upon the articular facet on the outer surface of the cricoid cartilage, a

movement of the one cartilage may take place on the other, round an axis passing transversely through the cricoid. By this movement, the crico-thyroid space may be enlarged or diminished according as the cartilages separate from or approximate each other in front.

Fig. 211.



A. Thyroid cartilage. *a.* The notch. *b.* Superior cornu. *c.* Inferior cornu. *d.* Slight prominence at median lines of inferior margin for the attachment of crico-thyroid ligament. *g, h.* Superior and inferior tubercles. *e.* Ala. *f.* Pomum Adami.

B. Cricoid cartilage seen from the side. *a.* Posterior superior margin. *b.* Articulating surface of arytenoid cartilages. *f.* Superior descending margin. *h.* The right surface articulating with inferior cornu of thyroid.

C. The right arytenoid cartilage. *a.* Base; position of the crico-arytenoid articulating grooves. *c.* lateral prominence at base, which gives attachment to the crico-arytenoideus lateralis and posticus. *d, b.* convex triangular surfaces for the attachment of the superior thyro-arytenoid ligaments. *f.* corniculum laryngis; between *f* and *e*, the posterior aspect of the arytenoid cartilage and concave surfaces giving attachment to the oblique and transverse arytenoid muscles. *g.* Vertical portion of cuneiform cartilage.

The *arytenoid* cartilages are two pyramidal bodies articulated by their bases with the oval articular surfaces, already described on the upper margin of the cricoid cartilage. Each presents a concave posterior surface in which is implanted the arytenoid muscle which passes from one cartilage to the other; an inner smooth surface covered by mucous membrane, and an outer surface which gives attachment to the crico-arytenoid muscles. From the anterior angles of the bases of the arytenoid cartilages proceed the vocal chords to be inserted into the angle of the thyroid. The mobility of the articulation of the arytenoids with the cricoid, and their connexion with the vocal ligaments give them great importance in the mechanism of the larynx.

The *cornicula* and the *cuneiform* cartilages are placed beneath the mucous membrane—the former at the apex, the latter parallel to the anterior border of the arytenoid cartilages.

The *Epiglottis* is a remarkable valve-like cartilage—in shape, like the spout of a ewer. It seems to issue from the angle between the alæ of the thyroid cartilage to which it is attached by a stalk-like ligament. It projects above the root of the tongue, and lies between that organ and the aperture of the larynx, like a valve, which is pressed over the glottis when the tongue is retracted. Its upper border is convex, and its posterior surface is concave, transversely convex in its length. It is a smooth and very flexible cartilage; covered by mucous membrane, but penetrated by holes and depressions in which are lodged the numerous mucous glands of the membrane that covers it.

Such is the skeleton of the larynx:—it hangs from the hyoid bone, suspended by the thyro-hyoid ligament and muscles, and, through the hyoid apparatus and some muscles, it is brought into connexion with the lower jaw and the base of the cranium.

Vocal Chords or Superior Thyro-Arytenoid Ligaments.—The various cartilages of the larynx are connected to each other by ligaments. Of these the most important and interesting, as being the essential part of the mechanism for producing vocal sounds, are the bands of fibrous tissue which extend from the anterior angle of the base of the arytenoid cartilages to the angle between the wings of the thyroid. These are the thyro-arytenoid ligaments, or, in physiological language, the *vocal chords.* They are bands of elastic ligament, extending between the points named (*t*, *v*, fig. 212). They do not, in the quiescent state, lie parallel to each other, but converge from behind forwards: their relative position, as well as their tension, can be varied to a considerable degree by reason of the mobility of the arytenoid cartilages. The length of the vocal chords is greater in the adult male than in the female—being as 3 : 2.

The elastic chordæ vocales are connected by an expansion of elastic tissue with the superior thyro-arytenoid ligaments, which are small bands of the same tissue extending from the apices of the arytenoid cartilages to the hollow angle of the thyroid, and separated from the inferior by a space called the ventricle of the larynx. These superior ligaments are likewise known as the *false chordæ vocales.*

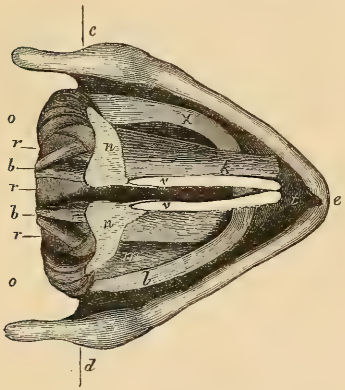
Much importance is attached by Lauth, Müller, and others to the fact, that many of the ligaments of the larynx are composed of elastic tissue, and connected together by a fibrous expansion of a similar structure. Lauth describes the elastic tissue of the larynx as starting from the angle of the thyroid cartilage between the

insertions of the thyro-arytenoid muscles, whence the fibres radiate downwards, obliquely backwards, and even somewhat upwards, forming a continuous membrane which passes to the cricoid and arytenoid cartilages, lines the ventricles of the larynx, and is connected with the crico-thyroid ligaments and the vocal chords, both true and false. The thyro-hyoid ligament is likewise elastic; and also the fibrous bands which connect the epiglottis to the thyroid cartilage and hyoid bone and the tongue. "If," says Müller, "we add to these parts the elastic longitudinal fibres in the membranous part of the trachea and bronchi, we shall have an idea of the great extent of the tissues susceptible of consensual vibration and resonance in the parts surrounding the organ of voice."*

The mucous membrane of the larynx is part of the great respiratory tract, described at page 162, and possesses the same anatomical characters at many points, being covered by ciliated epithelium. It is involuted to a considerable extent, forming numerous glands which cover the epiglottis, and are scattered over the interior of the larynx.

We have seen that the cricoid cartilage may move freely on the thyroid, or *vice versa;* and the arytenoids may be moved in various directions on the upper border of the cricoid. Moreover, suspended, as it is, loosely in front of the pharynx and œsophagus, the whole apparatus of the larynx may be moved freely up and down in the neck, approximating, or receding from the lower jaw. For these various movements the larynx is provided with two sets of muscles—the *extrinsic,* by which the whole organ is moved, and the *intrinsic,* destined to regulate the movements of the various segments.

Fig. 212.



View of larynx from above, after Willis. *b.* Ligaments uniting arytenoid and cricoid cartilages. *c.* and *d.* Direction of axis on which the thyroid cartilage turns. *e.* Thyroid cartilage. *k.* Left thyro-arytenoid muscle; right removed. *l, v, x.* Cricoid cartilage. *m.* Right crico-arytenoid muscle. *n.* Arytenoid cartilages. *o.* Crico-arytenoidic-postici muscles. *r.* Posterior part of cricoid cartilage. *t. v.* vocal ligaments.

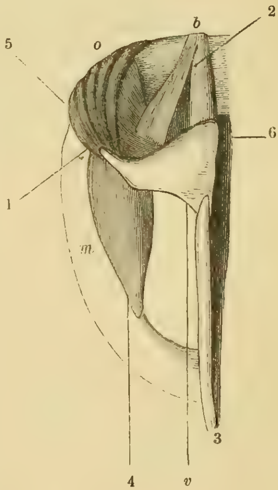
* Müller's Physiology, by Baly, vol. ii., p. 1005.

The *extrinsic* muscles are those which connect the larynx to the sternum below and the hyoid bone above: the sterno-thyroid, the thyro-hyoid, and, indirectly, the sterno-hyoid, omo-hyoid and stylo-hyoid, and stylo-pharyngeal muscles.

The *intrinsic* muscles are the crico-thyroidei, the arytenoidei, the crico-arytenoidei-postici and laterales, and the thyro-arytenoidei. We must refer to works on descriptive anatomy for the details of the connexions of these muscles; it must suffice here to state, that their names denote very accurately their attachments to the segments of the larynx upon which they can exert their force.

Action of Laryngeal Muscles.—The arytenoid cartilages are attached by ligaments to the posterior surface of the cricoid, which permit a considerable extent of rotation upon an articulating surface formed on the summit of the latter; by this arrangement the chordæ vocales may be stretched or relaxed, and the aperture of the glottis increased or diminished according to the direction of the force which acts upon the arytenoid cartilages. The posterior crico-arytenoid muscles render the vocal cords more tense, but at the same time cause them to diverge from each other, and so the width of the aperture of the glottis is enlarged. On the other hand, the thyro-arytenoid muscles, by drawing the arytenoid cartilages towards the thyroid, relax the vocal ligaments, while the crico-arytenoidei laterales by causing the arytenoid cartilages to rotate inwards upon their axes approximate the vocal chords and diminish the aperture of the glottis. The arytenoid muscle draws the two cartilages towards each other and so tends to diminish the aperture of the glottis, especially at its posterior part.

Fig. 213.



Magnified view of internal parts of Larynx of right side, after Willis, showing actions of Laryngeal muscles.

1, 2. Axis of articulation of Arytenoid Cartilage. 3. Direction of force of Thyro-Arytenoid Muscle. 4. Direction of force of Crico-Arytenoideus Lateralis. 5. Of Crico-Arytenoideus Posticus. 6. Of Arytenoideus Transversus. *b.* Crico-Arytenoid Ligaments. *m.* Crico-Arytenoideus Lateralis. *o.* Crico-Arytenoideus Posticus. *v.* Vocal ligament.

These different movements are further accelerated or increased in extent by the action of certain other intrinsic and extrinsic muscles of the larynx.

Thus the arytenoid cartilages being fixed by the contraction of the arytenoid and posterior crico-arytenoid

muscles, the vocal chords will be stretched by the descent of the thyroid cartilage over the cricoid, a movement performed by the crico-thyroid and sterno-thyroid muscles. The thyro-hyoid muscle, by drawing the thyroid cartilage upwards towards the hyoid bone, will assist the action of the thyro-arytenoids and relax the vocal chords.

By the action of these various muscles, the tension of the vocal cords may be increased or diminished, and the size of the opening of the glottis regulated at will.

Modes of altering the aperture of the Glottis and the tension of the vocal cords.

Crico-thyroidei	stretch the vocal chords		govern pitch of notes.
Thyro-arytenoidei . .	relax and place the vocal chords in the position for vocalization . .		
Crico-arytenoidei postici	separate the front of the arytenoid cartilages . .	open glottis	govern aperture of glottis.
Crico-arytenoidei laterales	press together the front of the arytenoid cartilages	close glottis	
Arytenoidei	press together the back of the arytenoid cartilages		

Nerves.—The nerves of the larynx are derived from the *superior and inferior laryngeal* branches of the vagus. Those from the former are distributed to the mucous membrane, and to the crico-thyroid muscles, by the external laryngeal branch; those from the latter to all the other intrinsic muscles of the larynx. Both these nerves anastomose with each other beneath the mucous membrane, near the arytenoid muscles.

The inferior laryngeal or recurrent nerve has relations to the innominata artery on the right side, and to the aorta on the left, which often implicate it in aneurismal tumors, especially of the latter artery. These, by compressing, weaken and paralize the nerve and the muscles which it supplies, and give rise to those alterations of voice which are sometimes among the earliest indications of the formation of an aneurism within the chest.

Action of the Larynx and Theory of Vocalization.—In the little apparatus of vocal chords attached to moveable cartilages and bounded by a free space above (the laryngeal ventricles) and by a free space below (the tube of the trachea), in which they vibrate, are found the chief conditions necessary for the production of the vocal sounds over an extensive though variable range of pitch.

Although all physiologists are agreed that this apparatus is the seat of the production of vocal sounds, there has, nevertheless, been much difference of opinion as to whether the larynx should

be regarded as a stringed instrument, in which the sound depends upon the vibrations produced by the movement of the stretched strings, as a wind instrument in which sounds result from the vibration of the column of air within them, or as a reed instrument which developes sound by the vibration of one or more highly vibratile tongues acted on by a current of air passing over them.

By the mechanism we have described, the vocal cords are placed in a position favourable for the production of sounds by their vibration, and the pitch of the sounds so produced modified.

Professor Willis showed, that in an ordinary respiration the aperture of the glottis assumed a V form; and its lips are inclined from each other: the apex of the V is situated towards the thyroid cartilage. When sound is to be produced, the lips of the glottis are made to approximate each other, and their inner edges become parallel. If now a current of air be forced through the chink, a sound is produced, the pitch of which depends entirely upon the tension of the vocal cords. De Kempelin says, that in the production of sounds, the lips of the glottis are approximated to the one-tenth or one-twelfth of an inch. The chords in vocalization vibrate throughout their whole length; but no voice-sounds can be produced by the passage of air through the posterior portion of the chink of the glottis between the arytenoid cartilages. Even when the chords are in contact, sound is produced by the forcible transmission of air.

When the vocal chords are rendered tense, a high note is produced; when they are relaxed, a note of low pitch results. A greater number of sonorous vibrations takes place in the former case than in the latter. It has been shown, that in the case of stretched strings, the pitch of the note varies in direct proportion to the amount of tension, according to the law that the number of vibrations produced by strings of similar length varies in proportion to the square-roots of the forces which stretch them. A string stretched by a certain force will produce twice the number of vibrations, if the force be increased four times; or, if a stretched string is caused to vibrate, and so to produce a certain note, if four times the force be employed, we obtain a note which is the octave of the first, requiring for its production twice the number of vibrations. These results, however, cannot be obtained upon the larynx, so that, as Müller has proved, the production of vocal sounds in this organ cannot be compared with those produced in a stretched string.

The distinguished *Physician*, M. Savart, was among the most

active supporters of the explanation of the formation of voice, on the principle of wind-instruments. He likened the larynx to a bird-call, and referred the exact seat of the development of sound to the air contained in the ventricles of the larynx, which would be affected by the upward current from the trachea, just as the air in the cavity of the bird-call is by the current from the mouth. But, to pass over the argument, that it is very doubtful whether the bird-call can be referred exclusively to the class of wind-instruments, M. Savart's views are decidedly negatived, by the fact that in the class of ruminants the superior or false vocal ligaments are absent, and, consequently, the ventricle of the larynx.

Ferrein was the first to show by experiment, that vibration of the vocal chords was the essential cause of voice. His experiments, published in 1741, were performed on the dead larynx. By them he was enabled to show, that the note varied according to the length and tension of the vocal chords, the same laws regulating the production of sound by these chords as by strings which are thrown into sonorous vibrations by currents of air.

The most important experiments upon the production of vocal sounds are those of Professor J. Müller of Berlin, and of Professor Willis of Cambridge. Müller investigated the action of membranous bands, or of tongues formed of caoutchouc, in generating sound under the influence of a current of air. The human organ of voice is imitated by a tube, capable of being varied in length; to one end of this, are applied two membranous vibrating tongues, attached to the wall of the tube, but separated from each other by a chink, through which passes the current of air necessary for throwing them into sonorous vibrations. Willis employed a similar instrument.

The results of these experiments may be thus briefly stated—

1st. That elastic bands, forming the lateral boundaries of a chink, through which a current of air is driven by a pair of bellows, may be thrown into vibrations so as to produce sounds which resemble those of the human voice.

2nd. That for such vocalization it is necessary that these bands should have, in addition to a certain degree of tension, a particular position likewise. This, which is called by Willis the *vocalizing position*, consists in the parallelism of the margins of the bands. In the quiescent state, during breathing, the lips of the glottis are inclined from each other; but in the vocalizing position, or that necessary for the production of voice, they become parallel. In the former condition, the glottis is a triangular space, with divergent

sides and apex in front; in the latter, it becomes a simple slit, or nearly so, with parallel sides. In the human larynx, the thyro-arytenoid muscles, lying on the outside of each of the vocal chords, exercise a principal influence in determining their relative position, and in adapting them for vocalization.

3rd. If a tube be adapted to the membranous tongues, in such a manner that the air may play upon them through it, and may pass through another tube after it has acted upon them, an influence is exercised not only on the timbre of the sounds produced, but also upon the pitch, which varies with the length of either and of both. In the human organ of voice, the larynx and bronchi represent a tube prefixed to the membranous tongues and chordæ vocales; and the cavity in front of the inferior ligaments of the larynx, a tube placed below the tongues.*

The vocal sounds may be produced by blowing air from the trachea through the aperture of the glottis in a larynx removed from the dead body; and by adopting means to vary the tension and the relative position of the vocal chords, the phenomena of the voice may be very closely imitated. When air is thus blown through the glottis, the vocal chords being approximated, clear and full tones are generated. They are produced most readily and certainly when the posterior part of the glottis, situated between the arytenoid cartilages, is closed. A certain constriction of the glottis appears necessary, as, when it is too open, an indistinct noise is merely produced. The pitch of the note is determined by the tension of the vocal chords, that of both being equal; it is not influenced by changes in the width of the aperture of the

Fig. 214.

Diagram to show parts concerned in vocalization, and the character and shape of cavities above and below the vocal chords.

* The reader is referred for the detail of Müller's experiments to p. 988 *et seqq.* of Dr. Baly's Translation, vol. ii., and to Müller's separate work, Ueber Compensation der phys. Kräfte am menschlich. Organ,—Berlin, 1839.

glottis. By increasing the weight which stretches the vocal chords, the height of the notes is raised; on the other hand, the relaxation of the chords lowers the notes: a register of about three octaves may be formed in this way. Even after all the parts which lie over the vocal chords have been removed, these variations of sound may still be produced.

The action of the vocal organ in man appears to approach more nearly to that of a reed instrument than to a stringed instrument. The former is characterized by being provided with a flexible vibrating tongue, against which the air can be propelled so as to throw the tongue into vibration, and to excite a musical sound. Such is the mechanism in the organ-pipe, hautboy, bassoon, accordion, and other instruments; the form and disposition of the tongue, and the material of which it is made, differing in each instrument.

Chest Voice.—In the larynx, as before remarked, the note may be changed, by varying the tension of the vocal chords, provided they be parallel and sufficiently close to each other. When a high note is to be produced, the head is raised and the larynx elevated, in order that the vocal chords may be rendered tense; on the other hand, if we wish to sound a very low note, the chin must be depressed upon the chest, so as to facilitate the relaxation of the vocal ligaments. At the same time, the strength of the blast of air exerts a considerable influence upon the pitch of the note. In reed instruments, it has been found that the note can be rendered higher by increasing the force of the blast.

Falsetto Notes.—The sounds to which we have been referring are produced solely by the vibration of the chordæ vocales; modified no doubt by the epiglottis, soft palate, etc., and the laryngeal cavity below. These notes are all termed chest notes; but in man tones can be generated very different from those which can be imitated by experiments upon the dead larynx. These are the falsetto notes. The precise mode of their production is obscure. From the experiments of Müller and Lehfeldt, it is probable that these falsetto notes are produced by the vibration of the inner portion of the borders of the vocal ligaments solely. Magendie and Mayo accounted for them upon the view, that only half the length of the chords was thrown into vibration.

Mr. Bishop has shown, that in the transition from the chest note to the falsetto note the crico-thyroid chink opens, having been closed immediately before, during the production of the highest note of the chest voice; so that the vocal ligaments become relaxed,

a change which necessarily follows must take place, if they are to produce a similar note, by vibrating only along half their length.

Singing.—In singing, a certain succession of tones is produced in definite order by altering the character of the glottis, just as by varying the conditions under which the air is thrown into vibrations in musical instruments we are enabled to alter the nature of the note.

The different varieties of the voice are arranged according to the pitch, which depends upon the length and other conditions of the vocal ligaments, and they are comprised in the following classes: *Bass, Tenor, Alto* or *Contralto, Soprano*; the two former belonging to the male, and the two latter to the female sex. Besides these, the *Barytone* is placed between the Bass and Tenor, and the *mezzo-Soprano* between the Soprano and Contralto. The compass of the voice varies from one to three octaves. Few singers possess a greater range of voice than the latter, but some of the most celebrated have much exceeded this—Catalani's voice included three and a half octaves. The compass of each kind of voice is shown in the following table:—

SOPRANO.

CONTRALTO.

C D E F G A B $C^1 D^1 E^1 F^1 G^1 A^1 B^1 C^2 D^2 E^2 F^2 G^2 A^2 B^2 C^3 D^3 E^3 F^3 G^3 A^3 B^3 C^4$

BASS.

TENOR.

Before puberty, the pitch of the male and female voice is nearly the same; but at this period the larynx of the male becomes larger and more prominent, and the vocal ligaments elongated, in virtue of which changes the pitch falls an octave in extent. In eunuchs this alteration does not take place, and they retain the puerile character of voice, which is, nevertheless, louder and stronger than in women. In men the vocal chords are one-third longer than in women, and the larynx is altogether much larger.

Unlike musical instruments, the human voice is capable of producing a vast number of notes, intermediate between the successive tones; and Dodart estimates the number of these which can be appreciated by the ear at three hundred.

Influence of the Nerves on Voice.—The inferior laryngeal and the crico-thyroid branch of the superior laryngeal, from the pneumogastric, are the sole channels through which the operations of the will affect the mechanism concerned in the production of the

voice-sounds, and as occurs in the case of other muscles, the movements of those muscles whose office it is to regulate the tension of the vocal chords, and govern the aperture of the glottis, are much more rapid and perfect, much more under the control of the will, and capable of executing more delicate movements in some persons than in others; and hence the wide difference between individuals as to their capacity for singing and vocalization. Something in the difference of vocalizing power is due to minute and inappreciable differences in the length of the vocal chords—size of glottis—quantity of the elastic vocal chord tissue—of the mucous membrane (slight affections of which create hoarseness).

The movements of the laryngeal muscles, as are the movements of respiration, are much influenced by mental emotions. In laughter, crying, sobbing, we have a combined excitement of respiratory and vocal actions.

In health, the emotions of grief, joy, and surprise, affect both voice and speech—the latter more frequently and intensely than the former. Diseases which involve more or less disturbance of the centre of emotions, affect both voice and speech. Hysteria, and chorea, may be referred to, the former generally affecting the production of voice, the latter of speech.

In certain affections of the brain, speech is impaired or altogether destroyed, or at most limited to a monosyllable *Yes* or *No.* This occurs under various conditions; sometimes in consequence of a chronic disease, sometimes of a shock: a diseased state of the convolutions or hemispheres is the most frequent concomitant of this symptom, but no precise part of the brain can be assigned as a special organ of speech.

In many diseases of a spasmodic or convulsive character, the action of the muscles of the larynx is affected. In the spasmodic croup or crowing inspiration of children, the chink of the glottis is frequently so firmly closed, and for so long a time as to endanger life. The peculiar "hoop" of hooping-cough, and the curious voice-sounds so common and so varied in hysteria, show that either these nerves themselves or the precise part of the centre with which they are connected, are influenced by the morbid action. In chorea the same want of power of co-ordinating the movements is observed in the little muscles of the larynx as in those which preside over the movements of the limbs and other organs.

In some of the conditions to which we have referred, it is difficult to say whether the motor nerve or its central origin is affected,

or whether the disturbance is not excited in the centre through the influence of an afferent nerve. Anything irritating the delicate mucous membrane of the larynx creates violent spasmodic action of the muscles of the glottis, in which those of respiration frequently take part, through the medium of the *afferent* superior laryngeal nerve.

Pressure upon the inferior laryngeal excites spasmodic cough, which often forms an important symptom of aneurism, or of mediastinal tumor. Section or disease of the inferior laryngeal nerve completely destroys the power of vocalization.

Stammering, at least in the greater number of instances, is an affection of the nervous system, not of the articulating organs. It consists in a defective control over the will, and an imperfect power of co-ordinating the muscles of speech. Stammering is much increased by any mental excitement, sudden surprise, etc., and one of the most important points to be kept in view in the treatment of this condition, is to avoid all cause of excitement to the patient, and to prevent him from thinking about his condition as much as possible, so that he may gradually obtain that command over the movements of the muscles, which is required for conversation.

Speech.—In the vocal apparatus, *notes* of very various pitch can be produced at will. The different sounds of the voice have been shown to be due to variations in the size of the aperture of the glottis and in the tension of the chordæ vocales. The vocal organ, however, is not capable of producing those articulate sounds by which we are enabled to communicate to each other our ideas; but this end is obtained by an alteration taking place in the cavity situated above the glottis, and in the position of the organs which it contains.

The most important conditions affecting speech are, first, the size of the oral aperture, secondly, the size of the buccal cavity, and, thirdly, the position of the tongue.

The production of vowel sounds, which are continuous and can be prolonged at will, depends entirely upon the size of the buccal cavity and outlet. In the sound of the *a* in *ah*, these are opened to their widest extent, while in sounding *a* in *fate* the buccal cavity requires to be much reduced in size, by the lateral expansion and elevation of the tongue. When we sound the *e* in *me*, cavity and outlet are made still less. The *o* in *no* results from a still further diminution of the oral aperture while the buccal cavity is much increased; and in the *oo* in *boot* the former is

contracted to a minimum, and the latter increased to its largest size.

The sounds just enumerated are the vowel sounds of continental languages, and they can all be prolonged for a time limited only by the passage of the air through the vocal apparatus. The English *i* may be looked upon as a diphthongal sound, and like the true diphthongs cannot be prolonged like a continued vowel sound. The diphthongal sounds appear to be produced by causing one particular vowel sound to pass into another with a considerable degree of rapidity—thus, *ou* is formed by the transition of the *a* in *far* to the *oo* in *cool*.

In the pronunciation of consonants, the soft palate, the tongue and lips more especially, take part; and in order to produce many of the sounds, it is necessary that the air should be forced through the passages suddenly, and often with a considerable degree of force, while others can be produced as continuous sounds like the vowels; hence the divisions into *explosive* and *continuous* consonants.

The former class includes the b, p, d, t, g, k,—the latter, the v, f, l, m, n, r, the sibilant consonants s and z, and the Greek θ (*theta*) *th*, which like *sh*, is a perfectly simple sound, and might be represented by one letter. The manner in which these sounds are produced by the alteration of the position of the organs concerned in the production of speech can be studied by every one in his own person; but for a full description of the position of the several parts concerned in producing them, the reader is referred to the works enumerated at the end of the present chapter.*

* For information upon subjects treated of in the present chapter, the student is referred to the following works:—Dissertatio de Loquela, 1700; Rev. Mr. Willis in the "Cambridge Philosophical Transactions," vol. iv., 1832; Lauth, "Mem. de l'Academie Royale de Médecine," 1835; J. Müller, "Elements of Physiology," translated by Dr. Baly; Articles, "Larynx" and "Voice," by Mr. Bishop, in the Cyclopædia of Anatomy and Physiology.

CHAPTER XXXII.

ON SECRETION.—SECRETIONS AND EXCRETIONS.—SECRETIONS WHICH ARE EXCREMENTITIOUS.—SECRETIONS WHICH ARE NOT EXCREMENTITIOUS, WHICH SERVE ULTERIOR PURPOSES.—VICARIOUS SECRETION.—INGESTA AND EGESTA.—ANATOMY OF SECRETING ORGANS GENERALLY.—OF THE GLAND CELL.—OF THE DUCTS OF GLANDS.

The function of *secretion* is that by which organised bodies *separate* from some portion of their internal or external surfaces a material which thereby becomes free or loose, and capable of removal, and which is likewise commonly known as the *secretion* from such surfaces. It is not sufficient that this material should be separated simply from the blood; for, if this were so, all the tissues would be secretions; but it must also be separated from a tissue of a special kind, hence known as a secreting tissue. The blood, then, furnishes the materials which are to form the secretions; but certain tissues are required, without which, these materials could not become secreted products: and the secreting tissues are anatomically arranged so as to have one surface adapted to set free, in the form of secretions, the materials derived on the opposite surface from the blood.

A secretion may be solid or fluid, living or dead, near to, or distant from, the constituents of the tissues in chemical constitution, capable of re-entering the blood, and being further serviceable in the economy, or, requiring to be expelled from the system as useless or hurtful. Thus, a great variety of very dissimilar products are conveniently classed together as secretions, in virtue of their being separated from the body by tissues provided for that purpose.

Excretions.—Some secretions consist mainly of substances resulting from the waste of the tissues coincident with their nutrition or renewal, and which are thrown off from the blood through the secreting surfaces almost as soon as the capillaries receive them from the tissues. Such are the urine, and portions of those matters

which escape in the form of fæces; and, allied to these, is the carbonic acid, which is eliminated, without the intervention of a true secreting tissue, directly from the capillaries of the lungs. If these matters were retained, they would accumulate in the blood and tissues, and prove, sooner or later, incompatible with life; and even a simple delay or retardation in the process of their removal, to whatever cause it may be attributable, must be attended with grave consequences to health. It is, therefore, impossible to overestimate the importance of distinguishing these products from other secretions, and of acquiring the habit of considering them under one common head. They are known as the *excrementitious secretions,* or, simply as *excretions.*

The kidneys are organs through which a large portion of the blood is constantly flowing, and in which the general mass of that fluid becomes so far purified as to be freed from certain waste materials which have just been thrown into it by the muscular and other tissues. The blood which leaves the kidneys, though rendered venous by the nutrition of the glandular tissue itself, is more free than before to receive the refuse of the other parts. Hence the kidneys must be regarded as a depurating organ, subservient to the functions of other parts of the frame. To prove this, it is only necessary to extirpate the kidneys from an animal, or to see their function arrested by disease: in either case, the blood and tissues become more and more loaded by the urinary matters which continue to be formed in the body, and which should have been eliminated as soon as formed by the extirpated or diseased organs. So essential, indeed, to animal life, is this excretion of nitrogenised matters, resulting from the waste of the nitrogenous tissues, that it may be safely said to be universally present, and to have a kidney, or analogous organ, assigned to it, wherever animals exist having an arrangement of different and mutually dependent parts, on such a scale as to render the direct expulsion of the waste materials at the points where they are formed impossible.

The principal *excretions* may be thus enumerated:—1. *Carbonic acid gas*, formed by the action of the oxygen upon carbon, and separated by the lungs; its accumulation in the blood is very rapidly fatal to life. 2. *Urea*, *uric acid* (in herbivorous animals *hippuric* acid), *kreatine,* and *kreatinine*: all nitrogenized principles of definite composition, resulting principally from the waste of the tissues, and eliminated by the kidneys; their retention in the blood is soon, but less rapidly, fatal. 3. Various *saline matters,* separated by the kidneys and skin. 4. *Lactic acid,* principally by the skin.

5. Certain portions of the *bile*, already considered (see p. 258, vol. ii.), by the liver. To these may be added sundry constituents of the fæces, of imperfectly known composition, but supposed by Liebig to be imperfectly oxidized matter,* escaping by the mucous lining of the intestinal tract, probably by the tubes of Lieberkühn and by the solitary glands; and lastly, also, whatever substances are taken in as food and absorbed into the blood, but which fail to be assimilated, either from their being superfluous in quantity, or incapable of serving any purpose in the œconomy.

Secretions which are not composed of excrementitious Substances, and which serve important Offices in the Œconomy.—Other secretions (and this is a large and diversified class) do not consist of waste materials, the results of the disintegration of the tissues, but are thrown off in certain situations where they are to perform a part useful or necessary to the protection or preservation of other organs, or of the whole body, or of the species. Of these, speaking generally, it may be said that they are *formed*, as well as eliminated, by the several organs which furnish them; that they retain more or less resemblance, in chemical constitution, to the food and the nutritious parts of the blood; and that, in many respects, they are allied to the living tissues of the body from which they are separated.

The highest example which can be given of these qualities is that of the male and female elements, the semen and the ova, which go to form the new being, and which are the production of organs essentially secreting. Here the secreted matter retains its organized form and its living properties, which latter are of so elevated a character, as to end in the development of an entire organism like that which has furnished the secretion.

Other examples, in which these qualities meet less decidedly, are presented by the milk, and by some of those secretions which have been already considered under the head of the digestive function, such as the saliva, the gastric juice, and the pancreatic fluid. These are poured out to mingle with the food, and variously to facilitate its entry into the blood; and there can be no doubt, that after having duly effected this object, they become in a considerable measure themselves reabsorbed with the food, so as to be further

* The fæces have lately been subjected to chemical investigation by Dr. W. Marcet, who has discovered an organic crystalline substance of an alkaline reaction, to which he gives the name of *Excretine*, an acid olive-coloured substance, of a fatty nature, *Excretolic acid*, and a fatty acid, having the properties of Margaric acid, but not constantly present.—"Proceedings of the Royal Society," vol. vii. No. 6.

serviceable for a time in the ever-moving circle of the functions of vegetative life. There is no waste here; and we may suppose that they do not become finally expelled until they have been reduced to forms of combination in which they can no longer minister to the life of the tissues. Such secretions are conveniently classed together as *recrementitious.*

But it would be an error to suppose that all matters separated from the natural surfaces of the body fall exclusively under one of the foregoing heads; on the contrary, it happens in some cases that a secreted product is of a mixed kind, partly excrementitious and partly recrementitious—partly rejected as needless or injurious—partly thrown off that it may subsequently fulfil a useful purpose in the œconomy of the individual and species. Thus the bile contains certain matters which are expelled with the excrements, while a large proportion of its elements is reabsorbed into the blood, after their commixture with the chyme in the intestines, and thus furnishes material for the production of animal heat in respiration.

The chief *secretions serving an ulterior purpose*, and which are thrown out with that object, are the following:—The generative elements—the milk, the salivary, gastric, pancreatic, and allied fluids; parts of the biliary fluid; the mucus from some surfaces; the epidermis and its appendages from the skin; the sebaceous and odoriferous matters from certain glands; the tears.

Water, as it forms a necessary part of the living frame, and is probably in constant course of formation within it, and as it is, besides, continually received in large quantities as food and drink, is a constant ingredient of the secretions, being thrown off especially by the lungs, skin, and kidneys. By the two former its loss is determined, in a great degree, by simple evaporation into the surrounding air; and this is necessarily influenced much by the hygrometric state and other conditions of that medium. By the latter, whose office is complemental of that of the preceding, a special apparatus is furnished for draining off the water, while this fluid is made useful in extracting the ingredients of the most important of the excretions from the surface over which it is subsequently made to flow.

Vicarious Secretion.—It has been remarked, that there is a sort of compensating action between the skin and kidneys in the normal condition of the system, dependent upon variations in temperature and other conditions. A similar power exists, in a more limited extent, in other secreting structures, by virtue of which

one organ may take upon itself the work of another, whose healthy function has been temporarily suspended or impaired by disease. Advantage is taken of this circumstance in the treatment of kidney diseases, in which the functions of those organs are temporarily or permanently impaired. In such cases, the removal of the urinary constituents is promoted through the skin, or from the intestinal tube, by giving purgative medicines, and by promoting secretions. The excretion of biliary matter in the urine in cases of jaundice, and the separation of the menstrual fluid from the mucous membrane of the lungs or stomach, are familiar examples of this vicarious action. Very numerous cases of metastasis of the urinary secretion are on record; and elements of the urine have been met with in vomit, in the stools, in the tears, and secretions of the ears and nose; in the milk, and upon the cutaneous surface generally, particularly about the navel.

If the kidneys of an animal be extirpated, the elements of the urine may be detected in many situations in which they are not normally present. In disease, when the functions of the kidneys are much impaired, it is not uncommon for the elements of the urine to pass off from the stomach by vomiting.

Ingesta and Egesta.—It is obvious, that if the weight of the body remains the same, the quantity of matter removed by the different excretory channels will exactly correspond to the ingesta, although the arrangement of the elements will be changed.

The proportion in which the different elements entering into the composition of the food are removed by the various secreting organs is shown in the following table, the result of some excellent experiments of M. Barral:—

Ingested as Food.		Excreted.		
		In Urine.	In Fæces.	By Lungs and Skin.
Carbon . .	21,770·4 grs.	1060·7	798·3	19,911·4
Nitrogen . .	1,649·0	756·6	142·0	750·4
Hydrogen . .	3,370·6	213·1	122·0	3,035·5
Oxygen . .	16,446·7	563·6	467·8	15,415·3
Total . .	43,236·7	2,594·0	1,530·1	39,112·6

The quantity of water removed from the body was usually one-fifth or one-sixth more than that taken in, showing that water is really produced in the organism.

General View of the Anatomical Plan of Secreting Organs.—We have said that the secreting tissues are arranged in such a manner

in the body as to have an external anatomical position, so as to be able to set free the secreted product when formed. Some organs of a strictly secreting kind, pour their material directly into the blood. It appears most reasonable to regard the whole lymphatic system as an apparatus of this description, calculated not merely to restore to the circulating current the superfluous or altered plasma, thrown by the capillaries into the interstices of the tissues, but destined by its glandular parts especially to act on the passing fluid, and to pour into it additional secreted matters, which pass by the efferent vessels to blend with the general mass of blood. The inner surface of the lymphatic vessels is here the external free surface, to which we refer as that from which the secretion is liberated.*

Again, there are other organs, viz., the synovial and serous membranes, which are usually and correctly classed as secreting organs. They have been already described (vol. i. p.126). The fluid they secrete seems furnished for the purpose of lubricating their surface, so as to facilitate motion. It, consequently, does not leave the surface on which it becomes free, but remains in contact with it, and only undergoes the same slow renewal and absorption, as all other solids and fluids with which blood in motion is brought into close contiguity. We have no reason to suppose that the effusions on these surfaces suffer much deterioration by their continued contact. They appear to differ but slightly from the serum of the blood, contain the same saline matters in solution, and in nearly the same proportions. The epithelium of these surfaces is no doubt concerned in furnishing these fluids, but exerts little catalytic power over the liquor sanguinis, which, consequently, is little altered by being secreted. Mr. Rainey has well pointed out that the epithelium in certain situations is developed in a particular manner upon the projecting folds and fringes of synovial membrane, known as glands of Havers; and has shown it to be probable that the viscid synovia owes its origin chiefly to the surface of these parts. He has found this disposition not only in the joints, but also in the sheaths of tendons, and in the bursæ mucosæ.†

But, dismissing these structures, we arrive at that great system

* This view results from Professor Goodsir's anatomical researches, and from considerations which have been ably stated by Dr. Carpenter.—See ante, p. 275.

† Proceedings of the Royal Society, May 7, 1846.

of parts, which we have before designated the mucous system, including, under one common title, the skin, mucous membranes, and true glands; the term, *true glands*, meaning those which, by a duct, or otherwise, pour their secretion on the external surface, and not into the blood. For a summary account of the tissues forming this order of parts, the note at p. 162 of the present volume should be referred to. The skin, and most of the great regions of the mucous membranes, together with some of the glands, have been already minutely described in different parts of the preceding pages; and it now only remains, before passing to a description, in detail, of the great remaining glands, to offer some observations on the general plan or scheme of structure, discoverable in these special organs of secretion.

Between skin, mucous membranes, and glands, there exists every gradation of structure, by which one can be conceived to pass into the other. They are modifications of a common type. The two former are secreting organs, in an expanded form, sometimes presenting glandular involutions in their thickness. But, in proportion as the glands differ from mere membranes, we find them assuming a more solid form, gathered up, as it were, into a more compact mass, in which are to be still recognised all the elements of the simple membrane in their true relative positions — the free surface being still the free surface, though now forming, it may be, the lining of ducts, and composing the internal tubular, or follicular recesses of the solid organ,—and the deep, or vascular surface preserving the same relation as before to blood-vessels, lymphatics, nerves, or areolar tissue, under its various modifications. In particular, the epithelium, or proper glandular tissue, remains capable by its anatomical position in regard to the external surface, to discharge its product on that surface. Thus the epithelium of the parotid gland, the liver, or the kidney, has such a relation to the remote parts of the excretory ducts of those organs, as that the secretion, resulting from the mutual action of that tissue and the blood, is set free into those channels, which are, in reality, continuations of the integument, and, therefore, in one sense, portions of the external surface of the body.

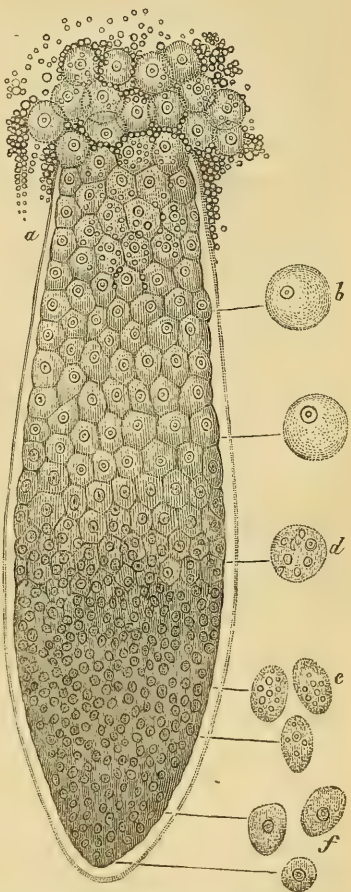
It will be readily seen how close and intimate must be, in all cases, the proximity of the glandular epithelium to the ducts. In fact, in many instances, the epithelium of the ducts is beyond doubt the secreting tissue, and the gland is a congeries of finely divided passages, or ducts, whose epithelium (though in a modified form) is

directly continuous with that of the outer surface, on which the duct opens. This, for example, is the case in the sweat glands, in the sebaceous glands, already described (pp. 422, 423, vol. i.), and in the kidney. But in other instances, whether owing to the form assumed by the terminal extremities of the duct, or, to an actual difference in the arrangement of the glandular epithelium, the greatest difficulty exists in determining the exact nature of the anatomical relation of the glandular and ductal epithelium, and of ascertaining whether they are continuous at all times or only at certain periods when the secretion is discharged. For example, in the salivary glands, the pancreas, and some others, the terminal parts of the gland are vesicular, while the ducts are tubular. Vesicular terminations of the ducts may be rendered apparent by mercurial injection; but it is by no means easy to demonstrate the permanent continuity of the epithelium lining or filling these vesicles with that which lines the ducts.

It is probable that most or all gland-follicles were originally closed vesicles. This has been shown by Dr. Allen Thompson to be the case in the early condition of the gastric glands; and Henle applies this view to other gland-structures. In his beautiful investigations upon the testicle of Squalus Cornubicus, Professor Goodsir has shown that the primary or mother cells are developed by the growth of isolated nucleated cells attached to the side of the duct. These cells grow and become the future acini, being connected with this duct by a hollow pedicle; in their interior, secondary cells, in which the spermatozoa are developed, appear. Still the mother cell is a closed cavity, and separated from the duct by its original wall. At length it gives way at this point and discharges its progeny of cells, containing spermatozoa, into the duct. The follicles then appear to become atrophied. There is another class of gland-structures, in which, according to this view, the mother cell remains persistent after it has discharged its first progeny of cells, and continues to produce successive generations of cells; the development of these cells commencing at the cæcal extremity of the follicle. The point at which they originate is looked upon by Professor Goodsir as the persistent nucleus of the original parent cell; and it is termed by him, the "germinal centre." Although it is scarcely possible to demonstrate the existence of this germinal centre in the gland-follicle, there are many instances in which this view certainly appears to be borne out by the structure of the part when subjected to a careful microscopical examination.

In the accompanying drawing of one of the cæcal tubes of the liver of the cray-fish (astacus affinis), after Leidy the gradual transition from the granular matter at the bottom of the follicle to the perfectly formed cells which are being discharged from its summit is well seen.

Fig. 215.



a. Cæcal biliary tube of Cray-fish. At *f*, *e*, *d*, *c*, *b*, are shown cells in different stages as they advance from the lower part towards the outlet. After Leidy.

In the glandules of Peyer, already described (ante p. 233), it would seem that vesicles form underneath, but in immediate contiguity with, the mucous membrane, and becoming filled with glandular contents, having the nature of nuclei, exhibit a great proneness to burst, and liberate their contents, perhaps periodically, on the free surface of the membrane. The ova, too, are very generally elaborated in the first instance in a matrix, or stroma, placed beneath, and not upon, the surface from which they are to be discharged. But, notwithstanding these differences, which will be further considered, it must be borne in mind that the gland-cells, or secreting elements, in the true glands, are always so placed as to be able to discharge themselves or their products on the outer surface.

Of the Gland-Cell.—The gland-cells select and separate from the blood the substances which form their secreted product. These elements form, in fact, in a certain sense a part of the food or pabulum of these secreting cells, which is set free when the cell has arrived at maturity, either by its rupture or by its complete detachment from the surface upon which it has grown, or, as occurs in other instances merely by transudation through its walls upon one side, while new matter is supplied to it from the plasma upon the other. Thus the function of secretion bears a certain analogy to nutrition. The cells in both processes select from the blood certain elements adapted for their

growth; but in secretion, these separate products, after having probably undergone some changes in the cell, are destined soon to be cast off, and no longer form an integral part of the organism; while, in nutrition, these elements serve to keep up the integrity of the structure by which they have been appropriated. It may be remarked, that the period of existence of the secreting cell, or the length of its life, varies considerably in different organs. Sometimes a very short time is sufficient for its development, growth, and decay; while in other instances, it may persist for a long period of time. Some of the most important modifications of secreting cells will be described under the head of the glands, into the composition of which they enter.

Of the Ducts of Glands.—Ducts are tubular, usually branched passages, forming continuations between the secreting tissue of the glands and the surface of skin, or mucous membrane, on which the secretion is eventually poured. They are a contrivance by which a large mass of secreting tissue, packed in a small solid space, can discharge its product at a given point. They often present dilatations, wherein the secretion may be delayed for a time, and where, in many instances, it may undergo changes; and they very commonly contain a layer of unstriped muscle in their walls, by whose agency their contents are propelled in the proper direction, often against gravity. This contractile tissue is sometimes developed at their orifice into a sphincter muscle. It is only the minuter glands which open directly on a surface, (*e.g.*, those of Lieberkühn or Grew, in the intestinal mucous membrane), which are without a duct.

The walls of ducts present, most internally, an epithelium and basement tissue, continuous with those of the skin or mucous membrane. Outside, there are (when present), the muscular coat and the areolar tissue, which is prolonged upon their exterior in a modified form. Bloodvessels and nerves ramify upon and within the latter coats. We owe the best description of the anatomy of ducts to Henle.

The epithelium may vary from the scaly to the columnar or glandular variety, and it is sometimes ciliated. The most common is the columnar, particularly in large ducts. In immediate connexion with the proper mucous tissue, comes the muscular element, arranged in two sets of fibres, one longitudinal, the other circular, of which, the latter can usually be seen to be the more internal. The fibrous elements are commonly nucleated, and resemble those of the muscular coats of bloodvessels; then follows areolar tissue,

forming an outer coat, together with bloodvessels and nerves. The areolar coat gives strength, toughness, and elasticity to the duct; the bloodvessels serve for its nourishment, and the nerves supply its muscular coat, and endow it with a peculiar sensibility, which, under particular circumstances of pressure or detention (as in the passage of a biliary or urinary calculus), may rise to the height of the most exquisite pain, reacting fearfully on the whole nervous system.

The smaller ducts very generally are without muscular parietes, and are reduced to a homogeneous basement membrane, lined with epithelium. Indeed, there is reason to believe that in some cases the very smallest consist either of simple epithelium or of mere basement tissue. The lobular passages of the lungs are an example of this latter constitution.

It is not difficult to prove that the larger ducts are muscular. Take for example the ureter. Open a small animal, just killed for the purpose, and this canal will be seen to present occasional peristaltic contractions, passing rapidly from the kidney to the bladder, which may be easily excited by a mechanical or galvanic irritation if they do not appear spontaneously. Besides this peristalsis, they undoubtedly undergo, like the bloodvessels, a slow and uniform dilatation and narrowing according to the bulk of their contents, or other conditions.

In some of those dilatations of the gland-ducts, which are provided for a temporary reception of the secretion, such as the urinary bladder and the vesiculæ seminales, the muscular coat attains such a thickness as to allow of being readily shown. The muscularity of the coats of the urethra was demonstrated for the first time some years ago by Mr. Hancock. In the gall-bladder, muscle is certainly developed to a far less extent; but even here, Dr. G. H. Meyer states, that by means of a powerful galvanic battery, he has caused this receptacle in the ox to contract, so as to diminish its capacity one-fourth. The Fallopian tubes, uterus, and vagina are parts rightly falling under the head of gland-ducts, though wonderfully modified in accordance with the functions they have to perform. The uterus, in particular, under the condition of pregnancy, offers an example of the highest development of the involuntary or unstriped muscular fibre-cells anywhere met with.

We shall now proceed with a description of those glands which have not yet been treated of. Of those pertaining to the alimentary canal, the salivary glands and their secretion (vol. ii. p. 182), and the secretion of the pancreas (p. 246) and the liver (p. 256), have been already spoken of, and the structure only of the two

latter remains to be considered. The kidneys and their secretion will follow; and we shall defer the consideration of the glands relating to the reproductive function to the chapters devoted to that subject. Such are the ovaries, the testes, the prostate, Cowper's glands, the mammæ.*

* The following works may be consulted upon the subject of secretion:—Articles, "Secretion," and "Mucous Membrane," in the Cyclopædia of Anatomy and Physiology. "Anatomical and Pathological Observations," Professor Goodsir, 1845. "Lectures on Nutrition," Professor Paget. Medical Gazette, 1847. "Principles of Human Physiology," Dr. Carpenter.

CHAPTER XXXIII.

SECRETING GLANDS.—OF THE PANCREAS.—OF THE LIVER.—THE LIVER IN INVERTEBRATA. — LOBULES OF THE LIVER. — PORTAL CANALS.—PORTAL VEIN.—HEPATIC ARTERY.—HEPATIC DUCT.—GALL BLADDER. — HEPATIC VEIN. — NERVES AND LYMPHATICS.—LIVER CELLS.—OF THE CONNECTION OF THE SMALLEST DUCTS WITH THE LIVER CELLS. — OF THE PASSAGE OF THE BILE INTO THE DUCTS. — OF THE QUANTITY AND USES OF THE BILE.

Of the Pancreas.—This is a large gland, placed across the spine, behind the stomach, in physiological relation with the duodenum or the first portion of the intestine. It is flattened from before backwards. Its left extremity, or tail, tapers off towards the spleen; its right extremity, or *head*, is much larger, lying close within the curve of the duodenum, and presenting a recurved extremity following the lower portion of that intestine, and sometimes termed the lesser pancreas. The ordinary weight of the pancreas, according to Cruveilhier, is from 2 to 2½ ounces, but may rise to 6 ounces. Its colour is gray, inclining to pink.

The pancreas, like the salivary glands, is imbedded in areolar tissue, and receives its blood from several neighbouring vessels. Its arteries are derived from the splenic and hepatic branches of the cœliac axis, and from the superior mesenteric. The blood is returned by the corresponding veins into the vena porta. Its nerves come from the solar plexus.

In structure, the pancreas appears to resemble the salivary glands. It is subdivided into lobules separated by septa of areolar tissue, which dip inwards from that which forms a common envelope to the whole gland. The lobules are subdivided into smaller parts by similar, but less complete and more delicate inflections of the areolar tissue; and these minute ultimate granulations or acini of the gland, correspond to the terminal extremities of the common duct. The excretory duct is concealed within the substance of the gland, and takes a course from the left to the right extremity, receiving very numerous tributaries on its way, and thus increasing

in size, till it joins the common bile duct, close to its entrance into the duodenum. At its termination it is as large as a crowquill. Its coats are thin and extensible, its internal surface smooth. It frequently happens that the duct belonging to the lower end of the curved portion or lesser pancreas opens separately into the intestine. In the rabbit the pancreatic duct opens by a separate orifice, sixteen or seventeen inches lower down the intestine than the bile duct (p. 250).

It is not difficult to inject the duct, and through it the ultimate secreting structure of the pancreas, with mercury. This may be best done in some of the smaller mammalia, where the glandular tissue is disseminated in lamellated grains between the layers of the mesentery, and where consequently the ramifications of the duct are naturally spread out towards the ultimate acini. The metal easily penetrates to these parts, and appears in the form of clusters of minute globules, having an average diameter of $\frac{1}{500}$ of an inch. These indicate, with probable truth, the terminal vesicles in which the duct ends, and which are lined with the epithelium, or true secreting tissue, continuous with that of the duct.

The vesicular terminations lie in the meshes of the capillary network, as is the case with the follicles of the salivary, and other conglomerate glands.

The secreting cells are more or less spheroidal in form, and vary somewhat in character according to their age. The mature cells are about the $\frac{1}{1500}$ of an inch in diameter, and are opaque, in consequence of being filled with numerous minute oil globules. The young cells are smaller than these, and are not so opaque.

The epithelium in the large ducts is of the columnar variety. The wall of the duct appears to be composed of fibrous tissue, in which elongated nuclei make their appearance upon the addition of acetic acid. The secretion of the pancreas has been described in chapter xxv. p. 248.

Liver.—The liver is a large solid glandular organ, of firm consistence, of a dark reddish brown colour. It measures about twelve inches from side to side, and six or seven inches from its anterior to its posterior border. According to the observations of Krause, the bulk of the liver corresponds to about eighty-eight cubic inches; its weight is between three and four pounds, and in the adult usually amounts to about 1-36th of the weight of the whole body; but in the fœtus it is comparatively much larger. The female liver weighs somewhat less than that of the male. The specific gravity of the liver is about 1·05 in health.

The following is an analysis by Prof. Beale of a liver, presumed to be healthy. The organ was taken from the body of a man thirty-one years of age, who was killed by falling from a second-floor window while in the enjoyment of perfect health.

		Per 100 of Solid Matter.
Water	68·58	
Solid matter	31·42	
Fatty matter	3·82	12·16
Albumen	4·67	14·86
Extractive matter	5·40	17·18
Alkaline salts	1·17	3·72
Vessels, etc., insoluble in water	16·03	51·01
Earthy salts	·33	1·05
	100·00	

In disease, the proportion of these constituents is liable to very great variation. In fatty degeneration, an enormous amount of fatty matter may accumulate in the organ. In one remarkable case, analyzed by Dr. Beale, the liver contained 75·07 per cent. of solid matter, and of this 65·19 consisted of fatty matter.* In scrofulous degeneration of the liver the albuminous materials and the water are increased, while the fatty matter is diminished in quantity.

The liver is situated in the right hypochondrium, and reaches over to the left, being thick and indented behind where it crosses the projecting bodies of the vertebræ, convex on its upper surface where it lies in the hollow of the diaphragm, and concave below where it rests against the stomach, colon, and right kidney. It is covered to a great extent by the peritoneum, the reflexions of which on to neighbouring parts, serve as ligaments to bind it in place, as well as to allow of the entrance and exit of the nerves and vessels, some of the latter being sufficiently large and strong to aid materially in the mechanical support of the organ.

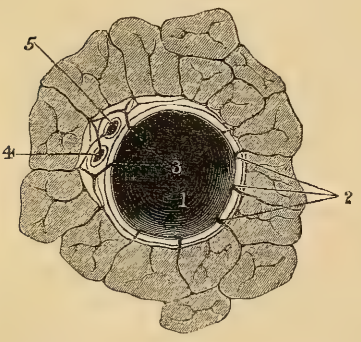
The liver is an unsymmetrical organ. In the fœtus, it is situated more equally on each side of the median line of the trunk; but in the adult the right side enormously preponderates, by the wasting or want of development of the left. It is still, however, divisible into a right and left lobe by the broad peritoneal ligament above, and by the longitudinal fissure beneath, both of these commencing in front by a notch in the border, across which passes, between the layers of the broad ligament, the cord-like remnant of the umbilical

* Diseases of the Liver. Dr. Budd. Second edition, 1852.

vein, and both tending towards the notch in the posterior border which lodges the vena cava; these divisions, however, are both of them on the surface only, and are rather vestiges of the imperfect conditions of fœtal existence than of value in the study of the physiological anatomy of the gland.

On the under surface of the liver, is observed a groove passing off from the longitudinal fissure, transversely, for a certain distance, on the surface of the right lobe, and lodging the biliary ducts, the sinus of the vena porta, the hepatic artery, with lymphatics and nerves, all enveloped in areolar tissue, called the capsule of Glisson, and brought to this *transverse fissure* between the layers of the gastro-hepatic omentum. From this groove, there extends throughout the substance of the organ a series of tubular passages, so numerously ramified and uniformly distributed, that no part whatever of the hepatic substance is at a greater distance from them than about the thirtieth of an inch. These are called the *portal canals* (fig. 216), so named by Mr. Kiernan, because they lodge the *branches of the portal vein*, from which the plexus of capillaries surrounding the biliary-cells takes origin. The portal canals also lodge the bile-ducts, which are thus conducted to that aspect of the mass of bile-cells, where the capillary plexus commences. The same canals also convey the hepatic artery with the lymphatics and nerves of the liver.

Fig. 216.



A transverse section of a small portal canal and its vessels, after Kiernan. 1. Portal vein. 2. Interlobular branches. 3. Branches of the vein, also giving off interlobular branches, termed by Mr. Kiernan vaginal branches. 4. Hepatic duct. 5. Hepatic artery.

On the posterior border of the liver already referred to, is a deep groove placed obliquely, *the fissure for the inferior vena cava*; from this there penetrate the substance of the organ, another series of ramified tubular passages, which are completely occupied by a nearly corresponding number of branches of the *hepatic veins*, or *venæ cavæ hepaticæ*, which open into the vena cava. These canals, called by the same distinguished anatomist, *hepatic venous canals*, are so distributed throughout the organ that some part of them comes within $\frac{1}{30}$ of an inch of every portion of its substance, and they are intermediate to the ramifications of the portal vein. The bases

of the lobules adhere to these veins, and when they are cut across they do not collapse. The hepatic veins occupying these canals, throughout the organ, receive the blood of the portal vein after it has traversed the plexus of capillaries which envelopes the series of biliary-cells. This plexus of capillaries we therefore term the *portal-hepatic plexus.* It is a plexus containing venous blood, from which the bile-cells derive the materials which they secrete. The space which the blood passes over in traversing this plexus, in contiguity to the cells, is measured by the distance between the *ramified portal surface* and the *ramified hepatic venous surface* of the liver. The series of bile-cells discharge the bile into the biliary ducts on the portal side of the plexus, i.e., where the blood is entering it, and their most remote parts commence on the hepatic venous side of it,

Fig. 217.

Human liver in which the portal vein (*d*) had been injected white, the artery (*e*) red, and the hepatic vein (*c*) lake; from the surface. Magnified 15 diameters. The capillary plexus is only shown in a few places. *a.* Portion of portal hepatic plexus. *b.* Portal hepatic plexus receiving at its portal surface small branches from the artery. *c.* Branches of the hepatic vein, interdigitating with the portal canals. *d.* Branches of the portal vein. *e.* One of the branches of the artery; some of its branches are seen ramifying upon the coats of the portal vein, and a few join the capillary plexus *b.* Dr. Beale.

i.e., where the blood is leaving it, so that the blood circulates in the reverse direction to that in which the bile must flow.

The Liver in Invertebrata.—The liver is one of the most constant glandular organs, being met with, in some form, in all animals provided with a digestive cavity. In the *polyps*, the liver is represented by some coloured cells round the stomach. In many of the *annelids*, clusters of biliary cells are seen surrounding the cæcal prolongations of the digestive cavity. In the Eolis (one of the nudibranchiate gasteropodous mollusks) a somewhat similar arrangement is observed, the follicles of the alimentary tube being prolonged into the papillæ, covering the dorsal surface of the animal. In most other *mollusks*, however, the liver exists as a distinct organ, and is composed of branched follicles, arranged round terminal ducts. The follicles contain coloured cells, in which oil globules are often present in considerable number. In many of the *crustacea*, the liver is detached from the intestinal walls, and consists of numerous large cœca (Fig. 215), which pour their contents into small ducts, although in others it seems to consist simply of cells arranged in follicles, which are connected with the intestine, as in the lowest classes. In *insects*, the hepatic organ takes the form of simple or branched tubes, from two to six in number, which open into the intestine. According to our observations, the cells do not appear to be arranged round the tube, so as to leave a distinct central channel, as in the uriniferous tubule, but lie within the basement membrane, without order or regularity, often completely filling the tube, and not unfrequently, from their large size, causing it to bulge. We shall presently see that a very similar arrangement exists in the tubular network of basement membrane, which contains the liver-cells in vertebrate animals.

Throughout the whole animal series, the liver consists essentially of cells containing colouring matter, and usually oil globules, which lie within a tube or follicle of basement membrane, continuous with the alimentary canal.

Having premised these general points, we shall now proceed to consider the anatomy of the liver more in detail.

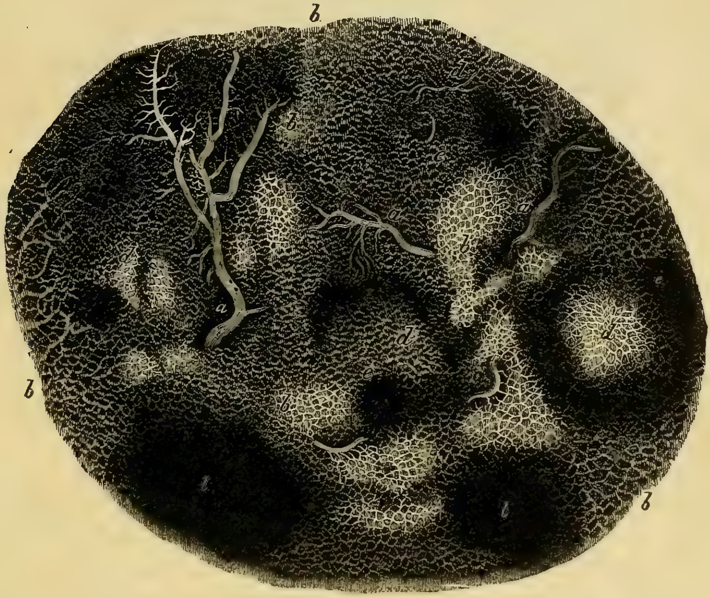
Lobules of the Liver.—The terminal twigs of the portal veins and the commencing radicles of the hepatic vein, thus distributed through the liver with a definite thickness of capillary plexus with nucleated bile-cells interposed, are further arranged in such a manner as that the intervening mass is gathered, not into a folded sheet, but into a great number of small portions, termed *lobules*. These lobules are apparent to the eye in many animals; but in the pig they are each of them invested by a separate and distinct membranous envelope or capsule, which is composed of delicate fibrous tissue (Fig. 218). In this animal, each lobule may be regarded as

Fig 218.

Portion of fibrous capsule of a lobule of the pig's liver, showing arrangement of the fibres—215 diameters.

an isolated and separate liver, and the whole gland as an agglomeration of smaller ones, connected by the penultimate branches

Fig. 219.



Lobules of a cat's liver, partially injected through the portal vein, and also through the hepatic vein. *a*. Twigs of portal vein. *b*. Capillaries springing from them, which serve to mark the outline of the lobules. *d*. Capillaries in the centre of the lobules injected from the hepatic vein. *e*. Situations at which the injection forced into the two vessels has met. *l*. Central parts of lobule not injected.

of the portal vein, artery and duct, which run between the lobules, and by the areolar tissue which accompanies them; but not by any inosculation or coalescence of the ultimate secreting elements, the liver-cells, or the capillaries. In other animals, and in the human subject, the lobules are not thus isolated, but are only imperfectly marked out by the several points of their exterior, to which the ultimate twigs of the portal vein and duct arrive. The twigs of the vein terminate in a plexus of capillaries common to all the contiguous lobules, and continuous between them, so that the lobules themselves have no definite limit (Fig. 219), but blend with each other, except at certain points of their exterior. It is not likely that these differences in the isolation of the lobules in various animals are of any physiological importance, but they have, probably, given rise to much of the difference of opinion which exists among anatomists on this subject.

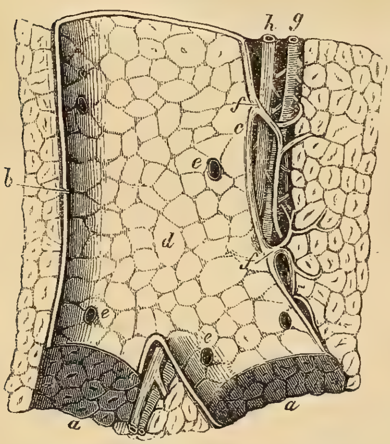
The shape of the lobules, whether completely defined by an investment of fibrous tissue, or merely mapped out by the position

of the several twigs of the portal vein, hepatic artery, and duct, may be said to be determined by the mode of distribution of these vessels. The *intralobular* hepatic vein occupies the central axis of the lobules, and usually consists of a stem, into which three to five, or even more, subordinate twigs empty the blood derived from the capillary plexus. The lobule is elongated on this vein, and presents a process for each of the subordinate twigs.

In all cases, the terminal branches of the portal vein and the duct arrive at the surface of the lobule at several points; and the surface of the lobule, whether complete or incomplete, is continuous with that of the portal canals. From this surface, in all cases, the capillary plexus tends by the slight elongation of its close meshes and converges towards the intralobular hepatic vein in the axis of the lobule. It probably follows, that in this latter situation the blood, after having been nearly deprived of those constituents from which the bile is formed, circulates more rapidly than at the more external parts of the lobule, whither it has just been brought by the portal veins, richly charged with these constituents.

Portal Canals.—It has been already observed, that the portal canals contain a branch of the portal vein with a branch of the hepatic artery, and of the biliary duct — not unfrequently the vein is accompanied by two branches of the artery and duct.

Fig. 220.



Longitudinal section of a small portal vein and canal after Kiernan. *a.* Portions of the canal from which the vein has been removed. *b.* Side of the portal vein in contact with the canal. *c.* The side of the vein which is separated from the canal by the hepatic artery and duct with areolar tissue (Glisson's capsule). *d.* Internal surface of the portal vein, through which is seen the outline of the lobules and the openings of the interlobular veins. *f.* Vaginal veins of Kiernan. *g.* Hepatic artery. *h.* Hepatic duct.

The branches of the artery and duct are connected with those of the portal vein by areolar tissue, which is abundant in the transverse fissure of the liver, and in the larger portal canals, but in the smaller exists chiefly on that side of the vein where the artery and duct lie; while, as the vessels diminish in size, the amount of this areolar tissue becomes less until it entirely ceases where the small branches which supply the lobules are given off. This investment of areolar tissue, described under

Fig 221.

A small lobule from the pig's liver, showing *a*. the interlobular branches of the portal vein, and *b*. a portion of the lobular capillary network within the capsule injected. Each branch is seen to give off small branches on either side to the adjacent lobules. After Dr. Beale.

the name of Glisson's capsule, from its discoverer, has been stated by many subsequent writers, to be prolonged into every part of the gland, separating the lobules from each other, and forming an investment for each,—a description which we have failed to verify in every mammalian animal which we have examined, except the pig, where this areolar tissue is really prolonged between the lobules.

Portal Vein.—The large portal vein is formed by the union of the veins of the stomach and intestines, the pancreatic and splenic veins and the veins of the mesentery, omentum, and gall bladder. The portal circulation has been described in p. 347, and we have, therefore, only to describe the distribution of the vein in the liver. The branches of the portal vein may be said, in general terms, to be arranged round the lobules; but the branches upon different sides do not anastomose so as to encircle each lobule with a venous ring, as many authors, following Kiernan's diagram, have described and represented, but communicate with each other only through the intervention of capillaries. Even in the pig there is no vascular ring, although to the naked eye it might appear so. In the liver of the human subject, and in livers allied to it, small branches of the portal vein can often be traced from the interlobular fissures into the lobule, breaking up into capillaries as

they go. The arrangement of the branches of the portal vein round one of the smallest lobules of the pig's liver, with a few of the lobular capillaries injected, is shown in Fig. 221.

Hepatic Artery.—Many branches of the artery pass to the capsule of the liver, in which they ramify abundantly, forming a network having large meshes. These *capsular* branches and their anastomoses, are readily injected in the liver of the fœtus or child.

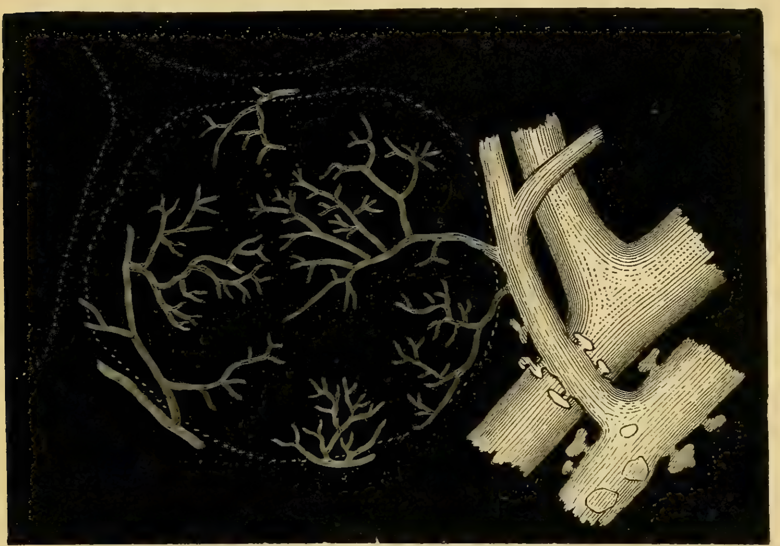
The artery gives off numerous branches in the portal canals. The greater number of these are distributed upon the coats of the ducts. The thick walls of the larger ducts are abundantly supplied with arterial blood; but the smaller branches of the duct, the coats of which are extremely delicate, pass through the meshes of an arterial network. In the pig this net-work may be demonstrated upon the surface of each lobule, Fig. 222, but in the human subject the branches are less numerous, and are seen only in the interlobular fissures; other branches supply the coats of the portal and hepatic veins. The greater quantity of blood, after passing through these small arteries, is collected by venous radicles which empty themselves into the branches of the portal vein. A few very small arterial branches may be traced from the portal aspect of the lobule for a short distance into its interior, where they join the portal hepatic plexus

Fig. 222.

a. Part of arterial ring, with branches ramifying upon the capsules of the lobules of the pig's liver. *b.* Arterial network. *c.* Portion of lobular capillary network injected from the artery and small branches of the latter entering it. After Dr. Beale.

of capillaries. The whole of the arterial blood, therefore, which supplies nutriment to the several structures of the liver,

Fig. 223.



A small lobule, shewing the duct branching upon the capsule, from the pig. The sacculi of the ducts are injected in this specimen. The vessel accompanying the duct is a branch of the portal vein.

passes through the capillaries of the lobule before it is returned to the heart, and no doubt furnishes a small portion of the matters from which the bile is formed. The artery was rightly regarded by Kiernan as one of the sources of the blood conveyed to the secreting structure of the liver, by the branches of the portal vein.

The gall-bladder is also supplied largely with arterial blood. The arteries are arranged so as to form a beautiful network. Each branch of the artery is accompanied by two branches of the vein, one on either side, and when the arterial and venous networks are injected with different colours a most beautiful appearance is produced. A similar disposition of arteries and veins occurs in the transverse fissure, and also in the large portal canals. This arrangement, has probably the effect of ensuring free circulation through the veins in those changes of size and position to which the vessels are liable.

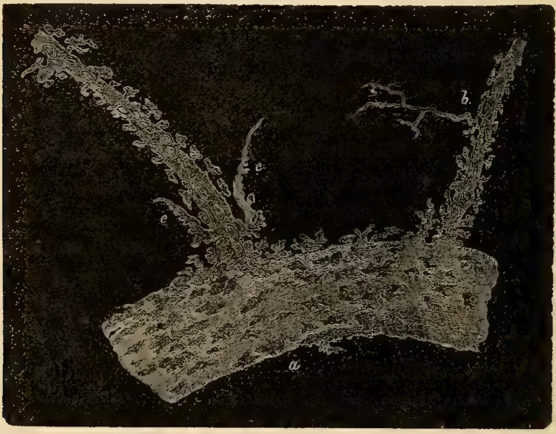
Duct.—At least one branch of the duct accompanies each branch of the portal vein, but frequently there are two or three. From the branch or branches accompanying the vein, several smaller ones pass off to the secreting structure. In the pig, the interlobular ducts, while running between contiguous lobules, are

applied, as it were, to the exterior of their capsules, and give off much smaller twigs on either side, which perforate the capsules, and become connected with the cells in the manner presently to be described.

Parietal Sacculi and Appendages of the Ducts.—In ducts of about the $\frac{1}{125}$ of an inch in diameter, and larger, there are many little saccular dilatations situated in the coats. These are the so-called glands of the ducts, and in the pig, and most other animals which we have examined, are arranged all round the tube. Dr. Beale, who has examined them with great care, describes them as, for the most part, simple oval pouches connected with the cavity of the duct by a very narrow neck, often not the $\frac{1}{5000}$ of an inch in diameter. In the larger ducts, they are branched, and often run for some distance in the coats. Occasionally, the branches of one gland anastomose with those of another. The largest are singularly complicated, and project some distance from the duct lying in the areolar tissue which surrounds it. Fig. 224.

In the human subject, a different arrangement occurs. Instead of being situated entirely round the tube, the openings form two rows or lines situated upon opposite sides of the ducts. The greater number of these openings are, however, the orifices, not of sacculi, but of small irregular tubes, which run obliquely for some distance in the coats of the duct and anastomose; some of

Fig. 224.



a. Portion of a large duct of the pig, injected with vermilion, showing the large cavities or glands in the coats of the ducts. The largest and most complicated are represented at *c*, just at the point where a smaller branch is coming off from the trunk of the duct. *b.* A small branch without glands. Magnified about ten diameters. From a drawing by Dr. Beale.

these branches leave the ducts and anastomose with each other just outside the trunk from which they are given off.

Many of the small ducts about the $\frac{1}{80}$ of an inch in diameter, have numerous cœcal pouches connected with them, arranged pretty close together, gradually becoming shorter as the duct becomes smaller, and giving off branches composed of basement membrane only. These irregular ducts with cœcal pouches are very numerous in the transverse fissure of the liver, where they form an intricate network connected with the larger branches of the duct in this situation. These were described by Theile as branching mucous glands, but were first noticed and named *vasa aberrantia* by Weber, who also described the anastomosis between the right and left hepatic ducts in the transverse fissure, by the intervention of these irregular branches.

In the portal canals, the vasa aberrantia occur as already mentioned, but in diminished number. Dr. Beale considers these cavities, or irregular branches, connected with the ducts, as little reservoirs in which the bile in ducts with thick coats is brought into closer proximity with the numerous vessels surrounding them, by which means it loses some of its water, and probably undergoes other changes. He observes, that the arrangement of the vessels around these ducts, both in the transverse fissure of the liver and in the portal canals, is similar to that which exists in the coats of the gall bladder. A small cavity with a narrow neck seems scarcely adapted for pouring out viscid mucus; moreover, the bile of animals, in which these so-called glands are very few in number, as in the rabbit, seems to contain as much mucus as that of the pig, in which animal the glands are very numerous and well developed. According to this view of their office, these cavities may be regarded in the light of little gall bladders.

The coats of the larger ducts appear to be principally composed of condensed fibrous tissue, but there is reason for supposing, that, at least in some of them, there are a few muscular fibre cells, although they do not form a distinct layer or muscular coat.

The epithelium of the larger ducts is of the columnar variety. The cells are large and well-formed, often exhibiting a distinct nucleus. They are frequently tinged with yellow colouring matter, and often contain yellow granules. In the smaller ducts, this epithelium becomes shorter, until, in the smallest branches, it approaches more nearly to the tesselated variety.

Gall Bladder.—The gall bladder may be looked upon as a diverticulum of the hepatic duct. It lies in a fossa underneath the liver. It is of a pear shape, and its fundus is directed down-

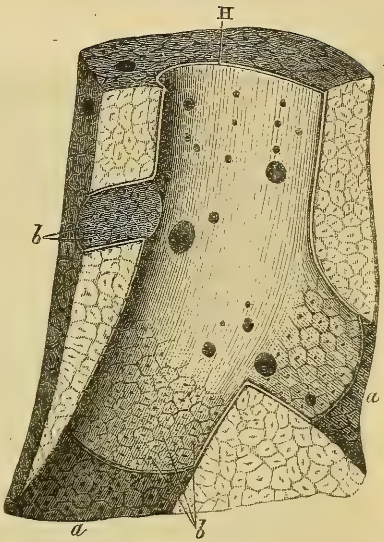
wards and forwards; it terminates in the *cystic duct,* which is about an inch in length. The *hepatic duct,* leaving the liver by the transverse fissure, passes downwards, and soon joins the cystic duct at an acute angle, to form the *ductus communis choledochus,* which is about three inches in length, and lies between the layers of the gastro-hepatic omentum. After coming into close proximity with the pancreatic duct, the common duct enters the coats of the intestine with the latter, and passes obliquely between them for three-quarters of an inch. The ducts open by an orifice common to both at the junction of the descending and transverse portions of the duodenum. The mucous membrane of the gall bladder is thrown into reticulated folds, which form the boundaries of numerous polygonal depressions, so that upon its internal surface it presents a honeycombed appearance. It is highly vascular, and is covered with columnar epithelium. The folds are prolonged into the cystic duct, where they are arranged in a crescentic manner, their general direction being that of a spiral, and they have been compared to a spiral valve. The peculiar arrangement of the vessels of the gall bladder has been already referred to. The cystic artery is derived from the right division of the hepatic, and the veins empty themselves into the vena portæ. The lymphatics are very numerous. The greater part of the thickness of the walls of the gall bladder is composed of fibrous tissue, but there also exists a thin layer of delicate muscular fibre cells, which take partly a longitudinal and partly a transverse direction. The human gall bladder is capable of containing about an ounce of fluid, but it undergoes great alterations in volume, and in it the bile becomes inspissated, and probably undergoes other changes.

This viscus is absent in many genera of fishes; in pigeons, toucans, and some other birds; in the elephant, stag, horse, and tapir; but it is present in the ox, sheep, and antelope. It is always found amongst reptiles. The reason of its absence in the animals above alluded to is not yet satisfactorily explained.

Hepatic Vein.—The branches of the hepatic vein run in channels, which are situated between the portal canals (Fig. 217), and in consequence of the small quantity of areolar tissue surrounding the hepatic vein, the bases of the adjacent lobules are in contact with it, so that when a branch of the hepatic vein is cut across, it does not collapse, but remains open. The small twigs which collect the blood from the lobules surrounding the trunk of the vein open at once into it, except in the case of the largest branches, where the coats are very thick. This arrangement is shown in Fig. 225, after Mr. Kiernan. In this drawing, the open-

ings of the small branches of the *hepatic* vein (intralobular vein) are seen in the centre of each lobule, while in Fig. 220, which represents a *portal* vein laid open, the orifices of the smallest branches are seen in the spaces between two lobules (interlobular veins).

Fig. 225.



Longitudinal section of an hepatic vein. *a*. Portion of the canal from which the vein has been removed. *b*. Orifices of ultimate twigs of the vein (intralobular) situated in the centre of the lobules, after Kiernan. Compare the arrangement of the small veins in this figure with the branches of the portal vein in fig. 220.

The capillaries in the central part of the lobule open into the small twig of the hepatic vein upon all sides. These points are well seen in the pig's liver, where the lobules are distinct, but in the human and other livers, the arrangement varies slightly in consequence of the lobules communicating with each other in the intervals between the interlobular fissures (Fig. 217).

Nerves and Lymphatics.—The nerves of the liver are derived chiefly from the sympathetic, but a few branches of the vagus are also distributed to the organ. They consist of tubular and gelatinous nerve fibres, and are distributed principally upon the walls of the artery over which they form a network.

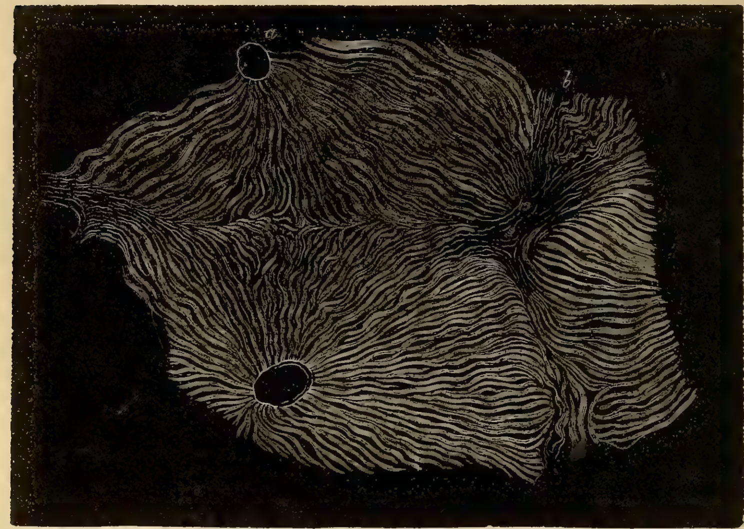
Branches may be traced into Glisson's capsule, and to the coats of the gall bladder and larger ducts, as well as to the coats of the larger branches of the hepatic vein.

The lymphatics are found in considerable abundance in the liver; they are distributed to the gall bladder, and form a network upon the surface of the organ underneath the peritoneum. An abundant network of lymphatics exists in the largest portal canals, and when the ducts are injected, it not unfrequently happens that a small branch bursts, and the injection escapes into the lymphatics. In this way, some lymphatic glands near the liver are often injected, and the injection sometimes even reaches the thoracic duct, as occurred to Mr. Kiernan, and also to Dr. Beale.

Of the Liver Cells.—From what has been already stated, with regard to the arrangement of the solid capillary venous plexus of the lobules, it will be inferred that the cells occupy the meshes of this

network. It has long been a question whether the cells lie amongst these capillary vessels, or are enclosed in a basement

Fig. 226.



Section of horse's liver, at right angles to branches of the hepatic vein, showing the cells forming lines radiating from the centre towards the circumference of the lobules, from a preparation of Dr. Beale's.

membrane, as we should expect from the analogy of other glandular organs. It has been admitted by all who have examined the liver carefully, that in sections made in a particular direction, the cells are seen to form lines which radiate from the centre towards the circumference of the lobule; these lines being connected with oblique or transverse branches. Such an appearance is not presented in every section, but only in those made exactly at right angles, with the small twig of the hepatic vein. This is well seen in fig. 226. The cells are described by Kölliker and others, as being placed end to end, forming solid cylinders, but not invested with basement membrane. Usually there is only room for one row of cells; but in some situations, two or three may be seen between two capillary vessels. Dr. Handfield Jones has been led by his researches to adopt the same conclusion with regard to the arrangement of the liver cells, and Dr. Carpenter has expressed himself in favour of a similar view.

On the other hand, Retzius, Leidy, and some other observers, advocate the presence of a tubular basement membrane, in which the cells lie, and which is continuous with the hepatic ducts.

The minute anatomy of the liver has lately been subjected to a careful investigation by our friend and former pupil, Dr. Beale; and we believe he has established the existence of this basement membrane by several different methods of preparation. His observations have been made upon injected as well as uninjected preparations. The membrane is so exceedingly delicate, that it can be demonstrated alone by the granular matter which adheres to it. Dr. Beale has succeeded in injecting the tubular network in which the cells lie; and the injection has been seen to pass round the cells, separating them slightly from each other. When the cells are broken down by the action of chemical reagents, the outline of the tube can often be seen distinctly. This delicate basement membrane in most situations appears to be incorporated with the walls of the capillaries, but in some places it is to be demonstrated distinct from them.

Not unfrequently cells are met with in the fluid surrounding a section of liver with shreds of membrane attached to them; and in a few rare instances this membrane may be seen in the form of a tube, in which the cell is evidently contained. Injection, however, affords the most satisfactory proof of the existence of this basement membrane. In well-injected specimens the outline of the

Fig. 227.

Portion of tubular network of basement membrane in which the liver cells lie, *a*. from an injected specimen—the shaded portions show the position of the injection. *b*. Cells and free oil globules lying within the tube. *c*. Specimen in which the cells have been disintegrated. From the pig; 215 diameters; after Dr. Beale.

tube in which the cells are contained can be seen in some parts of the lobule, separated from that of the capillary vessels.*

The liver cells may be broken down in some specimens, and the tubular membrane contain only granular matter suspended in fluid as represented in fig. 227 c.

The peculiar and characteristic cells of which the substance of the liver is chiefly composed, are of a more or less spheroidal form, but often somewhat flattened and many-sided from mutual compression.

They vary from the $\frac{1}{1000}$ to the $\frac{1}{2000}$ of an inch in diameter, and sometimes even smaller. Their surface is smooth, and their outline distinct and well-defined. Each contains a distinct nucleus in the interior, and occasionally cells may be observed with two nuclei. In the nucleus a highly refracting nucleolus, with several granules, can usually be distinguished.

The contents of the cell appear to be of a firm viscid consistence, so that when pressed between glass, the contents do not escape suddenly, but the whole cell becomes flattened. Usually there are, in the interior, several oil globules, which, as regards size and number, are subject to great variations. In some cells the entire cavity is occupied by globules, in others not one can be observed; besides oil globules, distinguished by their light centre and dark well-defined outline, the cell contains in its interior numerous amorphous granules, which may vary in size from a scarcely visible dot to a particle as large as a blood globule, or even larger. Granules of a bright yellow colour, composed of biliary colouring matter, are often met with, but do not occur constantly. In cases of jaundice from obstruction of the duct, the number and size of these coloured particles often increase to an enormous extent, so that the cell appears to be entirely occupied with them, and in extreme cases no distinct cells whatever can be detected.

In highly fed animals, and in that condition termed fatty degeneration of the liver, so common in cases of phthisis, the cells seem almost entirely occupied by large oil globules, without any coloured particles. The cells at the portal aspect of the lobule usually contain most oil, while those in the centre contain a greater number of coloured granules, but frequently these yellow granules are present in the cells in both situations.

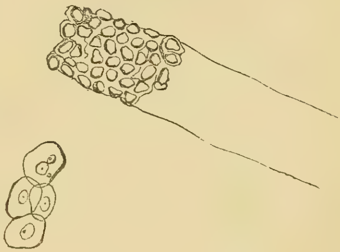
In dilute caustic soda, or potash, the cells swell up and become pale, and of a more rounded form; after a short time they are dis-

* These specimens were prepared by injecting the ducts with Prussian blue, and the portal vessels with plain size.

solved, unless the solution is very weak. Acetic acid produces a somewhat similar change, but the cell membrane does not appear to be dissolved. The nuclei always appear more distinctly defined after the addition of the acid; cells which, at first, were found to contain no coloured granules, by being soaked for some time in dilute acetic acid exhibited many.

Of the smallest Branches of the hepatic Duct and of their Connexion with the hepatic Cells.—Of the manner in which the ducts commence in the liver, there has been much difference of opinion, and the most conflicting views have been entertained. Mr. Kiernan considered that the ducts commenced in a lobular plexus although he was never able to prove the existence of such an arrangement. Kölliker gives a diagram to illustrate his view, which supposes that the open ends of the ducts impinge against the columns of the hepatic cells at the margin of the lobule. Dr. Handfield Jones traces the ducts to the same point, where, he believes, they terminate without having any direct communication with the hepatic cells; and he considers that the small cells in these ducts are alone concerned in the secretion of the bile (Fig. 228). If this view of the anatomy of the liver be correct, this large organ must be nearly related to the vascular glands.*

Fig. 228.



Terminal portion of interlobular duct, with epithelium within it. Four hepatic cells to show relative size. To illustrate Dr. Handfield Jones' view.

Dr. Beale's researches show that Mr. Kiernan's original view is more nearly allied to the truth.

In the interlobular fissures numerous finer branches leave the small trunk of the duct and pass towards the secreting cells. In the human subject, many of these may be followed for some distance without giving off branches or anastomosing with each other. These small ducts lie around the small branches of the portal vein, and their course is often tortuous.

In some animals, particularly in the rabbit, the small ducts anastomose, forming a network round the vein. This net-

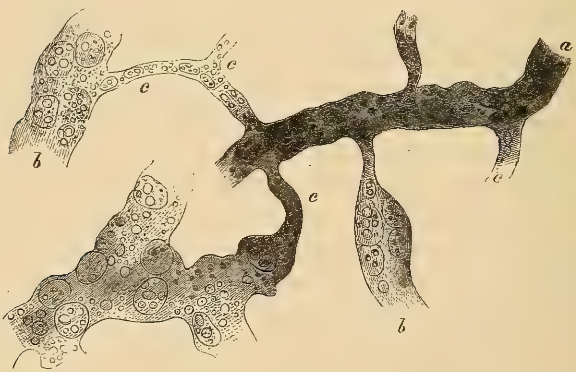
* Vide Kölliker's Manual of Human Histology, translated by Busk and Huxley; Sydenham Society, 1853-54. Dr. Carpenter's General and Comparative Physiology, 4th edition.

work is continuous with the network of the lobule in which the cells lie. In the human subject, and in most mammalia, the small ducts do not form a network in this manner, but pass off at once to the cell containing network with which they are continuous. In the pig, the smallest branches of the duct penetrate the capsule of the lobule at various points, and immediately become connected with an intimate network which lies immediately beneath it, and partly within its substance. This network may be regarded as the most superficial portion of the cell-containing network, and where the liver is fatty it contains cells distended with oil globules.

In the human liver, and in those of most animals, except the pig, some of the smallest branches of the duct pass for a short distance beneath the surface of the lobule, and become continuous with some of the branches of the cell-containing network in that situation. In a cursory examination these narrow ducts appear to lie amongst the cells without being connected with them. The greater number of branches, however, join the cell-containing network round the margin of the fissures.

Near to the point where the duct joins the cell-containing network it becomes very much narrowed, and is often not more than the $\frac{1}{4000}$ or $\frac{1}{5000}$ of an inch in diameter, and even less, in the uninjected state. Several of the narrowest ducts in the pig are represented in Fig. 229.

Fig. 229.



a. Small branch of interlobular duct—pig. *b.* Most superficial part of cell containing network, with cells filled with oil, and free oil globules. *c.* Narrowest portions of the duct. Magnified 215 diameters. The shaded parts show the points to which the injection reached. After Dr. Beale.

Fig. 230 represents some of the small ducts and a part of the cell, containing network at the surface of a lobule in the human

liver. The cells have been nearly destroyed by the action of reagents in preparing the specimen.

The epithelial cells which line these minute ducts approach to the tesselated variety. They are, for the most part, round or oval granular cells, some of them about the $\frac{1}{5000}$th of an inch in diameter, while others are less. They present very similar characters in the different animals which we have examined, and the same general arrangement of the minute ducts has been shown to occur in birds, reptiles, and fishes, with certain unimportant modifications.

Fig. 230.

Narrowest portions of the duct, lined by ductal epithelium, showing their connection with the cell-containing network. Close to the narrow ducts, a venous capillary and a small branch of the artery are represented in section. The liver cells have been destroyed by the mode of preparation. From an uninjected specimen of the human liver, magnified 215 diameters, after Dr. Beale.

The epithelium of the ducts does not pass by gradations into the secreting epithelium, but terminates at the point where the latter commences. The narrowing of the excretory portion of the tube is met with in many other glands, but in none is there a more striking contrast between the excretory and secreting portions of the gland, or between the epithelium lining the ducts and that by which the secretion is formed, than in the liver.

Of the Passage of the Bile into the Ducts.—If the view of the anatomy of the liver which we have described be correct, the secreting cells at the surface of the lobule are those which take the most active part in the secretion. These are the cells which the portal blood first reaches; and it is in this situation that the cells first show an increased quantity of oil globules within them in cases of fatty degeneration. The bile is not formed in the central part of the lobule and transmitted from cell to cell, as has been described by some authorities, but the bile formed by each individual cell escapes through the interstices between the cells until it reaches the duct. If it be urged as an objection to this view, that no visible interstices exist between the cells, it may be answered, that injection can be made to flow by these channels in a direction the reverse of that which the bile naturally takes, and, therefore, under the greatest disadvantage. There can then be no obstacle to the passage of the bile towards the ducts: moreover, the great changes in bulk which we know the liver cells so readily undergo, will readily account for the close contact in which they are often observed to lie.

From a careful consideration of the anatomy of the parts, we should be led to look upon the liver as a large gland in which a considerable quantity of a highly elaborated secretion was slowly formed, and slowly transmitted in a more highly concentrated form towards the intestine. The arrangement of the vasa aberrantia and of the little cavities in the coats of the thick-walled ducts, the abundance of vessels and lymphatics in such close proximity to the ducts, and the great similarity of their disposition with that of the vessels of the gall bladder, where we know absorption of fluid takes place, favour the idea that important changes occur in the bile after its formation by the cells of the liver.

The liver is, therefore, a true gland, consisting of a formative portion and a system of excretory ducts directly continuous with it. The secreting cells lie within a delicate tubular network of basement membrane, through the thin walls of which they draw from the blood the materials of their secretion.

Quantity and Uses of the Bile.—We have already considered the composition and uses of the bile in Chapter XXV.; but since that part of our work was published, some important results have been communicated by Bidder and Schmidt, which we shall here briefly allude to.*

These excellent observers have concluded, from numerous experiments upon different animals, that the quantity of bile secreted during the twenty-four hours is much larger than had been supposed. Cats secreted 14·5 grammes, dogs nearly 20 grammes, and sheep 25 grammes, for each kilogramme (about 2 lbs. 3 oz. avoirdupois) in the weight of the animal. From these data, it is of course difficult to draw a correct inference as to the quantity of bile secreted by the human subject; but, from calculating from these results, it has been rendered probable that an adult man secretes about 54 oz. of pure bile in the twenty-four hours, and this contains about 2½ oz. of solid matter. This estimate is very much higher than that which we have given at p. 253.

The activity of the secretion varies greatly at different periods of the day. For one or two hours after a meal, it is very small in amount; but from this time it gradually increases until it attains its maximum, about the fifteenth hour after the last meal. The secretion then rapidly diminishes in quantity, until it is not more than it was two hours after the meal. The gall-bladder empties itself about two-and-a-half or three hours after taking food.

* Die Verdauungssaefte und der Stoffwechsel von Dr. F. Bidder und Dr. C. Schmidt. Mitau und Leipzig, 1852.

It appears that an exclusively amylaceous, or fatty diet, causes a great diminution in the secretion of bile, while a pure flesh diet induces a very abundant secretion.

The presence of bile very much promotes the absorption of fatty matter, although a certain quantity of fat is absorbed even if no bile enters the intestine. The presence of bile causes the absorption of two-and-a-half times more fatty matter than would be absorbed without it. Bile appears to render the mucous membrane more permeable to fatty matter.

Bidder and Schmidt consider that the chief object of the bile is "to prolong the series of changes to which animal matter is submitted within the organism, and thus to render it for a longer time efficient in the discharge of vital processes."*

* On the Pancreas, consult article "Pancreas" in the Cyclopædia of Anatomy and Physiology, by Dr. Hyde Salter. Upon the anatomy of the Liver, the following works may be referred to :—Kiernan, "The Anatomy and Physiology of the Liver," Phil. Trans., 1833; Theile, Art. "Leber," im Wagner's Handwörterbuch der Physiologie; Article, "Liver," by Mr. Wilson, in the Cyclopædia of Anatomy and Physiology; Leidy, in the American Journal of the Medical Sciences; Kölliker's Mikroskopische Anatomie; Beale, "On the Ultimate Arrangement of the Biliary Ducts, and on some other Points in the Anatomy of the Liver of Vertebrate Animals," Phil. Trans. 1856.

CHAPTER XXXIV.

SECRETING GLANDS.—THE KIDNEYS.—PARENCHYMA.—MATRIX.—URINIFEROUS TUBES.—MALPIGHIAN BODIES.—CONVOLUTED PORTION OF THE URINIFEROUS TUBE.—STRAIGHT PORTION.—VESSELS OF THE KIDNEY.—OF THE SECRETION OF URINE.—URINE.—QUANTITY.—RE-ACTION.—CHEMICAL COMPOSITION.—UREA.—URIC ACID.—HIPPURIC ACID.—CREATINE.—CREATININE.—EXTRACTIVE MATTERS.—AMMONIACAL SALTS.—FIXED SALTS.—CHLORIDES.—SULPHATES.—PHOSPHATES.

Next in size and importance to the liver, are the kidneys. These glands are symmetrical organs, one being placed on each side of the spine in the lumbar region. In consequence of the position of the liver, the right-kidney is placed rather lower down than the left. These organs are surrounded by a varying quantity of fat, and are placed behind the peritoneum. The kidney is of a dark reddish brown colour, of a firm consistence, and of a close compact texture. Its general form is that of an ordinary French bean, compressed from before backwards, its convex border being external, and its concave edge, or hilum, where the vessels enter, looking towards the median line. The weight of the healthy kidney is from 4½ to 5 oz. in the male, and somewhat less in the female. The kidneys are supplied with blood by the renal arteries, two large trunks which come off at right angles from the abdominal aorta. The blood is returned by the large renal or emulgent veins which open into the inferior cava. These vessels, with the nerves for the supply of the organ, enter the kidney at its notch or hilum, whence also proceeds the ureter.

Of the Kidney in the lower Animals.—The first trace of an organ which can be regarded in the light of a kidney is met with among the *Polypi*, but the renal nature of this is at least doubtful. In *Porpita*, one of the *Acalephæ*, Kölliker has described an organ which contains guanin, and which he therefore looks upon in the light of a kidney. In the *Annelida* the existence of a renal apparatus is doubtful; but there is some reason for believing that the so-called respiratory organs are to be regarded in this light. The existence of

these glands is not determined in the *Crustacea;* but among the *Arachnida* tubes composed of basement-membrane, and containing epithelium, exist. Guanin also has been detected in them, so that there can be little doubt of their real nature. Among *Insects*, renal organs exist as long narrow tubes, and the presence of uric acid has been detected in several species. In the *Mollusca*, except in the lowest class, kidneys are distinctly observed, and are either two in number, or combined to form a single organ with an excretory duct. The spongy organs of the *Cephalopoda* have been proved to be true kidneys, and uric acid has been detected in them with the murexide test by E. Harless. Kidneys exist throughout the vertebrate classes, and are composed of tubular glands, provided with one or more efferent ducts, connected with which are often observed numerous appendages. The uriniferous tubule consists essentially of a tortuous tube of basement-membrane, lined with secreting epithelium, and dilated at its closed extremity, so as to embrace a tuft of highly-tortuous capillary vessels.

The specific gravity of the healthy kidney is about 1·050, but is liable to vary somewhat, according to the quantity of fluid which exists in the organ at the time of examination.

The following is an analysis of the cortical portion of a healthy human kidney by Dr. Beale. The organ was taken from the body of a healthy man, thirty-one years of age, who was killed by falling from a second-floor window:—

		100 parts of Solid Matter.
Water	76·450	
Solid matter	23·550	
Fatty matter, containing much cholesterine	·939	3·98
Extractive matter, soluble in water	5·840	24·79
Fixed alkaline salts	1·010	4·28
Earthy salts	·396	1·68
Albumen, vessels, etc.	15·365	65·24

Even in health, the proportion of water and solid matter varies greatly, which fully accounts for the varying statements of different observers with respect to the weight of the healthy kidney. In disease, the composition of the secreting structure of the kidney undergoes great alteration. The fat is very much increased in quantity in kidneys in a state of fatty degeneration. The relative proportion of the solids generally may be much diminished in quantity, which is remarkably the case in some specimens of enlarged kidney. The increase of size, in these instances, being accounted for by an unusual quantity of water in the tissue of the organ; but in many cases, it is, no doubt, dependent upon deposition of new matter. In a very large kidney, weighing half a pound,

only 14·39 per cent. of solid matter was present, so that in this instance the increased weight of the organ was undoubtedly due to a larger proportion of water than occurs in health, rather than to the deposition of any adventitious tissue, or to an increase of the normal gland-textures.

Surface of the Kidney.—The kidney is immediately invested with a firm fibrous coat, called the capsule, which is composed of condensed areolar tissue, and is continuous with the tissue constituting the matrix of the kidney, in the meshes of which the tubes ramify: some small vessels also connect the capsule of the kidney with the proper gland-structure. At the hilum, the capsule is continuous with the external or fibrous coat of the pelvis of the kidney and the fibrous coat of the ureter. The vessels also receive an investment from it at this point.

If the surface of the kidney be carefully examined, it is seen to be imperfectly mapped out into a number of small polyhedral spaces or lobules, in general appearance somewhat resembling the markings of the lobules of the liver. These markings are in part due to the arrangement of small branches of the veins which are spoken of, by anatomists, as the stellate veins. Commencing at the surface of the kidney, they penetrate the cortical part in a vertical direction, at nearly equal distances, and receive, in their course to the hilum, the blood from the venous plexuses surrounding the secreting tubes. In the spaces just described, may be seen the convolutions of some of the uriniferous tubes. No arteries reach the surface.

Ferrein supposed that the tubes formed little pyramids, each of which radiated from the *medullary* towards the *cortical* part of the kidney, the base of each pyramid consisting of one of these spaces or lobules. It appears, however, that although each pyramid contains many tortuous tubes, with their capillaries, the convolutions of a single tube are by no means confined to one pyramidal space.

Besides the apparent divisions into lobules just referred to, the surface of the kidney bears the vestiges of several fissures, marking it out into lobes which may be seven or eight or more in number; these lobes indicate the original condition of the kidney in intra-uterine life when they were separated from each other, and formed distinct renules. In the embryos of mammalia generally, the same arrangement is observed; and it remains permanent in the cetacea. In the kidney of the otter, seal, ox, and some other

animals, it is also conspicuous. In the ox, the division into lobes extends only to the pyramids.

Parenchyma.—The parenchyma of the kidney consists of two distinct portions; the one *cortical*, about half an inch in thickness, forming the whole convex surface of the organ, of a dark red colour, and to the unaided eye of a granular appearance, and exhibiting numerous red spots (Malpighian bodies) abundantly scattered through it. The *medullary* portion is embraced in this; it is pale and smooth, arranged so as to form several pyramids, varying in number from eight to fifteen; their bases are placed towards the cortex, from which may be traced a number of nearly straight lines, which converge towards the summit of the pyramid to which they belong. In this part of the kidney there are no Malpighian tufts, and even to the unaided eye, it appears to be composed of a number of straight converging lines or tubes.

These pyramids or cones end by free summits which project on the hilum into the pelvis of the kidney, the mucous membrane lining this cavity being continuous at the summit of the cone (or mamilla) with the tubes. The mucous membrane of the pelvis, however, forms a sort of fossa, or saucer-shaped cavity, around each mamilla, or termination of the pyramid. These calyces receive the urine escaping from the open orifices of the tubes on the summit of the cones, and convey it toward the pelvis; they become enormously increased in dimensions if there be any obstruction to the passage of the urine from the ureter or bladder.

Matrix.—With reference to the presence of a fibro-cellular matrix in the kidney, which serves as a support for the vessels and tubes, there has been much difference of opinion. It was originally described by Goodsir, and has since been noticed by several observers.

The matrix appears to us to be composed of a firm transparent and granular substance, in which we have seen small granular cells; but have not been able to ascertain their precise nature. The fibrous appearance seen in thin sections we believe, to be due rather to the crumpled state of the walls of the capillaries and uriniferous tubes, than to the existence of ordinary fibrous tissue in the matrix itself.

The intervals between the contiguous tubes and capillaries are greater in the pyramids than in the cortical portion of the organ, and consequently the matrix is more distinct in this situation; but

even here it has only a faintly granular appearance, and we have been unable to see any distinct fibres.

It appears to us that this structure is of little physiological importance; it probably serves as a support for the tubes and capillary vessels.

As the tortuous tubes in the cortex pass in and out amongst the interspaces of this matrix, portions appear to be circumscribed, as it were, giving the idea upon a section of a number of small cysts,* an appearance which is often very marked in certain cases of disease, when the tubes are enlarged. In the kidneys of many rodents, especially in that of the mouse, this appearance exists in a very marked degree, in consequence of the highly developed condition of the matrix in these animals; but, in all the instances alluded to, the true structure of this part, and often the continuity of the tube as it winds in and out, can be demonstrated with ease. A thin section of the cortical part of the kidney, made in any direction, displays these interspaces containing sections of the tubes, between which may often be seen vessels which have been cut across.

Uriniferous Tubes.—The uriniferous tubes, formerly termed tubes of Bellini, in which the characteristic elements of the urine are secreted, consist of two distinct portions, as already alluded to; the first, or highly *convoluted* part of the tubes, which is probably the sole seat of true secretion, and the *straight* portion, which is directly continuous with the former, and conducts the secretion towards the opening upon the mamilla, from which it passes into the pelvis of the kidney. In the other direction, the convoluted portion of the tube terminates in a dilated extremity, which completely invests the vessels of the Malpighian tuft.†

We shall now consider, first, the minute structure of the Malpighian bodies; secondly, that of the convoluted portion of the tube; and, lastly, that of the straight portion.

Malpighian Bodies.—The Malpighian bodies are met with in all vertebrata. In the mammalian kidney, where there exists a division into cortical and medullary portions, they are only found in the former. In an injected specimen, they appear, to the unaided eye, as coloured points abundantly scattered throughout the cortex of the organ. They vary much in size in different

* On Diseases of the Kidneys, by George Johnson, M.D.

† Phil. Trans., 1842.

mammalia, and are often larger towards the base of the cones. They are, for the most part, of a spherical, oval, or flask-like form. A small artery *afferent vessel* may be seen to enter the tuft, and a minute venous radicle *efferent vessel* to emerge from it in close proximity to the artery (Fig. 231). The Malpighian body itself consists of a rounded bunch of capillaries derived from the afferent and terminating in the efferent vessel, the former dividing over the surface, the latter emerging from the interior. This vascular tuft lies within a clear and perfectly transparent capsule, lined at its lower part with epithelium. The epithelium, which is continued upwards from the uriniferous tube into its flask-like dilatation, cannot usually be traced for more than about one-third of the length of the capsule (Fig. 3, p. 65, Vol. I.); but in the proteus (Fig. 232), the capsule is seen to be entirely lined with an exceedingly thin layer of delicate epithelium, the cells of which are of an oval, or polyhedral form, with a very large granular nucleus, and about the $\frac{1}{750}$ of an inch in diameter. The capsule itself consists of hyaloid membrane, which is directly continuous with the basement membrane of the convoluted portion of the tube. In fact, each uriniferous tubule terminates by a dilatation which embraces the vessels of the tuft, and is intimately united to them at the point where they enter and emerge.

Fig. 231.

From the human subject. This specimen exhibits the termination of a considerable arterial branch wholly in Malpighian tufts. *a.* Arterial branch, with its terminal twigs. At *a*, the injection has only partially filled the tuft. At β it has entirely filled it, and has also passed out along the efferent vessel *e f* without any extravasation. At γ it has burst into the capsule, and escaped along the tube *t*, but has also filled the efferent vessel *e f*. At δ and ϵ it has extravasated, and passed along the tube. At *m* and *m* the injection, on escaping into the capsule, has not spread over the whole tuft. Magnified about 45 diameters.

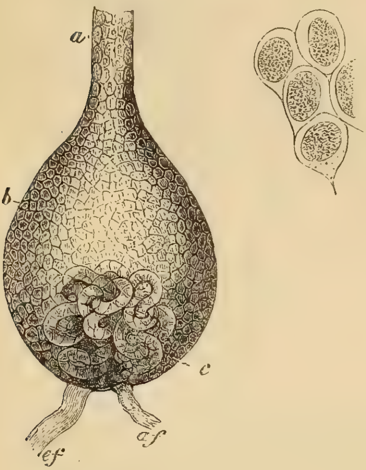
The continuity of the tube with the Malpighian capsule has

been proved in several ways. In specimens which have been carefully injected from the artery, not unfrequently it will be found that the coloured material escapes and extravasates from the vessels of the tuft into the cavity of the capsule, and thence runs down the tube (Fig. 231).

In disease, it is not at all uncommon to find the capsule of the tuft, and the tube itself, injected with blood, in consequence of hæmorrhage from the vessels of the tuft.

The difficulty of injecting the capsule by forcing injection from the pelvis of the kidney, cannot reasonably be urged as an objection to this view, for all who have had any experience in injecting the minute ducts of glands, will agree that it is in very few instances indeed that the injection can be forced to the termination of the tube. The epithelium within it is apt to be forced towards its cæcal extremity, and by its accumulation renders such a result impossible, while, in the majority of cases, the force requisite to overcome the resistance to the passage of fluid, along a highly convoluted tube in the reverse direction to that which its contents naturally take, is more than sufficient to cause its rupture.

Fig. 232.



Malpighian tuft; kidney of the Proteus anguineus, showing vessels lying within the capsule, the inner surface of which is entirely covered with a single layer of tesselated epithelium. *a.* Uriniferous tube. *b.* Capsule. *c.* Tuft of vessels which were injected in the preparation from which this drawing was taken. *a f.* Terminal twig of the artery. *e f.* Efferent vessel. Magnified about 50 diameters.—A small portion of the capsule, with its epithelial lining, is represented in the smaller figure, magnified 215 diameters.

The kidney of the horse is very favourable for demonstrating these points, and the double injection composed of acetate of lead and bichromate of potash will be found to furnish the most satisfactory results.

In the kidney of the frog, or of the newt, the continuity of the capsule with the basement membrane of the tube is exceedingly distinct and easy of demonstration. The tuft of vessels is seen lying naked within the capsule, uncovered either with epithelium or by any reflection of the basement membrane composing the capsule. In the frog, the neck of the tube close to and some way within the capsule is lined with ciliated epithelium, which con-

tinues in very active motion many hours after the death of the animal (vide Fig. 3, Vol. I.) In the newt, and in some snakes and other reptiles, the tube is completely lined with ciliated epithelium throughout; and by the activity of the motion, the epithelium can be traced for one-third of the way within the capsule. Ciliated epithelium has not yet been demonstrated in the kidneys of mammalia; but in one instance Gerlach has seen it in the kidney of the fowl. In various fishes and in many reptiles it is very frequently met with.

The statement of Gerlach and other observers, that the vessels of the Malpighian tuft are invested with epithelium, may be explained by the fact that small granular or nucleated cells may be frequently observed in connexion with the vessels. After repeated and careful observation, we are convinced that these cells are situated either within the vessel itself or enclosed in its wall (Fig. 233). In the tuft of batrachian reptiles, the white corpuscles of the blood often give the idea of being connected with the wall of the vessels, instead of lying in their interior. When the vessels are much shrunken, and their walls a little plaited, or corrugated, the appearance of cells lying upon the little capillary loops is produced when these loops are seen in profile. We have been able, in many instances, however, to demonstrate small oval or circular cells within the wall of the capillary vessel itself, and are inclined to look upon these as the nuclei of vessels. Here and there a granular cell may sometimes be detected on the surface, but they are very few in number and irregular in their arrangement; and we are satisfied that it cannot be regarded as a fact of any physiological importance, and that the vessels of the tuft are really bare within the capsule.

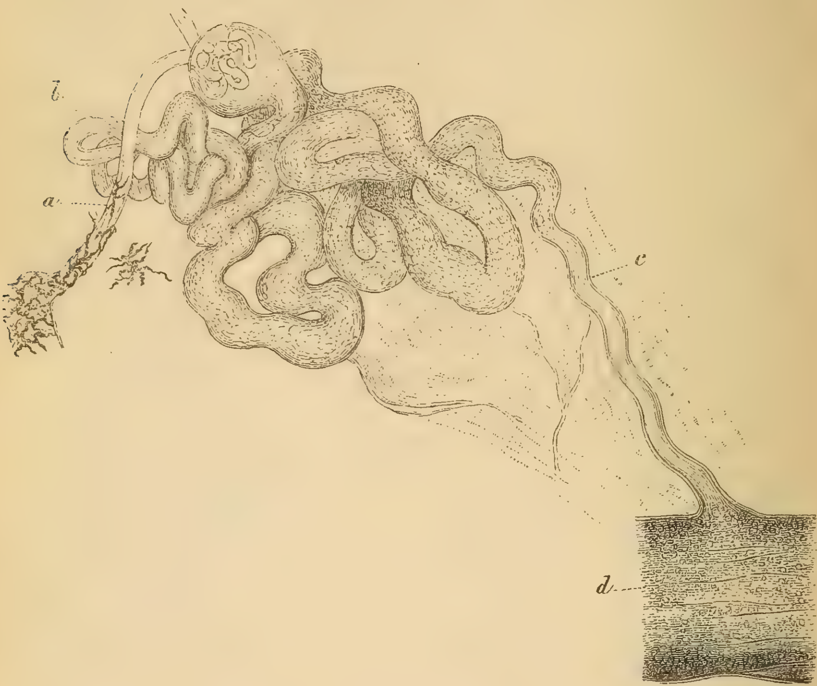
Fig. 233.

Small portion of a loop of capillary vessels of the tuft of the kidney of the large water newt (Triton cristatus), showing nuclei within the wall of the vessel. The line above the vessel is the outline of part of the capsule. magnified 215 diameters.

Convoluted Portion of the Tube.—From the capsule of the Malpighian tuft, we pass to the convoluted portion of the tube, which is directly continuous with it. This is composed of a delicate basement membrane, lined by epithelium. Externally, the basement membrane is in close contact and probably incorporated with the matrix of the organ; and it is in immediate relation with an abundant capillary plexus, which carries the blood after it has passed through the vessels of the Malpighian body. It is from this blood,

that the elements characteristic of the urinary secretion are selected by the epithelium lining this part of the tube. The diameter of the tube is less immediately after leaving the tuft, than in the rest of its course further down (Fig. 234). The epithelium in the con-

Fig. 234



Entire uriniferous tube of the large black newt (Triton cristatus, female). *a.* Artery having upon its walls numerous branched pigment cells. The commencement of the tube, and that part near the tuft, are of less diameter than the central portion, which is the most active part of the secreting tube. Towards its termination in the upper part of the oviduct, *d*, the tube becomes straight and much narrowed, *c*. Magnified about 30 diameters, from a drawing of Dr. Beale's.

voluted portion of the tube presents an excellent example of the spheroidal, or glandular variety. It consists of polyhedral particles rather less than $\frac{1}{1000}$ of an inch in diameter, with a distinct nucleus, and containing numerous granules, and occupying as much as one-third or more of the total diameter of the tube.

The extreme diameter of the convoluted tube is about $\frac{1}{450}$ of an inch, while the diameter of the central canal is not more than from $\frac{1}{1000}$ to $\frac{1}{900}$ of an inch.

Straight Portion of the Tube.—The straight portion of the tubes of which the medullary cones or pyramids are composed form anastomoses, or if traced from the papilla towards the base of the

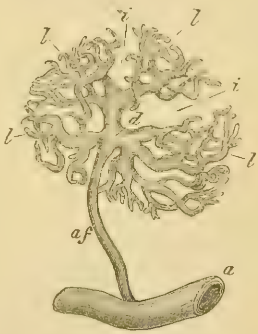
pyramid, the large tubes near the apex may be said to divide dichotomously, so that the number of the individual tubes, which would be seen in a transverse section, increases as we proceed from the apices of the pyramids towards their bases, while their diameter gradually diminishes. In the latter situation there may be many thousand tubes, while the number of openings upon the extremity of the mamilla are comparatively very few in number. The tubes at their orifices vary in diameter, from the $\frac{1}{300}$ to the $\frac{1}{200}$ of an inch, while towards the base of the pyramid they do not exceed $\frac{1}{600}$ of an inch. The aggregate capacity of the tubes at the base of a cone is enormously greater than that of the much smaller number of somewhat larger tubes at their orifices.

Fig. 235.

Transverse section of a pyramid of the human kidney, about a quarter of an inch from the papilla. *a.* Section of largest tubes. *b.* Section of smaller tubes, at a point previous to their opening into a larger one. The thin delicate epithelium approaching to the squamous variety, is seen lining this straight portion of the uriniferous tubes. *c.* Small vessels which ramify between the tubes in the transparent granular matrix, *d.* Magnified about 120 diameters.

The epithelium in this situation differs in character from that in the convoluted portion of the tubes; the cells are smaller, more transparent, and approach more nearly to the scaly or tesselated variety. They seem rather to serve as a protective layer than to share in the secreting function. The cells here are usually very thin, approaching to squamous epithelium in character; and although the total diameter of the tube is less than that of the convoluted portion, the diameter of the central canal is greater.

Fig. 236.

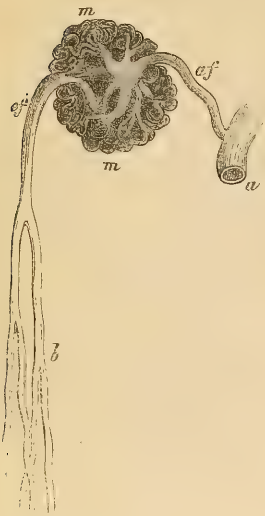


Malpighian tuft from the horse. The injection has penetrated only to the capillaries. *a.* The artery. *a.f.* One of its terminal twigs (or the afferent vessel. *d.* The dilatation and mode of breaking up of the terminal twig after entering the capsule. The division of the tuft into lobes, *l, l, l,* is well seen. *i, i.* Intervals between the lobes. Magnified about 80 diameters.

Vessels of the Kidney.—The renal arteries divide into four or five branches, which enter the kidney at the hilum between the vein and the ureter. These vessels are surrounded with a quantity of fat. They pass between the papillæ to the bases of the cones,

over which they spread. From these arteries smaller branches are given off, which ascend in the cortical substance nearly to the surface, and, in so doing, give off, on all sides, a number of small terminal twigs, the afferent vessels of the Malpighian bodies. Arrived within the capsule, the small afferent vessel at once divides into four or five branches, each of which again divides dichotomously. The small capillary vessels form loops, which project towards the opening of the uriniferous tube. The blood is received from these vessels, which lie towards the outside of the tuft, by branches of the efferent vessel which converge towards the more central part of the tuft to form one trunk, which leaves the Malpighian body, and soon breaks up into a plexus of capillary vessels, in the meshes of which the tubes lie. The terminal arterial twigs with their appended tufts, when injected with vermilion, have been compared not inaptly to a bunch of currants.

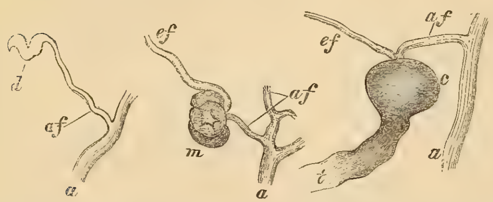
Fig. 237.



Malpighian tuft, from near the base of one of the medullary cones, injected without extravasation, and showing the efferent vein branching like an artery as it runs into the medullary cone. *a.* Arterial branch. *a f.* The afferent vessel. *m, m.* Malpighian tuft. *e f.* The efferent vessel. *b.* Its branches entering the medullary cone. Magnified about 70 diameters.

The size and complexity of the Malpighian bodies differ much in different animals, according to the activity of the function they are called upon to discharge. The vessels present fewer convolutions, the tufts are smaller, and their arrangement much simpler in those animals, in which the urine is almost of a solid consistence. Compare the complicated arrangement in the horse and other mammalia in figs. 236 and 237, with the few and simple convolutions in birds, fig. 238.

Fig. 238.



From the parrot; injected by the artery. *a, a, a.* Terminal branches of the artery. *a f, a f, a f.* Terminal twigs of the artery. *d.* Dilatation of the terminal twig on entering the Malpighian capsule. *m.* This dilatation more completely filled, showing its convoluted form; and, *e f, e f,* the efferent vessel. *c.* The Malpighian capsule filled by extravasation from the contained vessel, and the tube *t* likewise filled. Magnified about 80 diameters.

By reference to the following table, it will be seen that the diameter

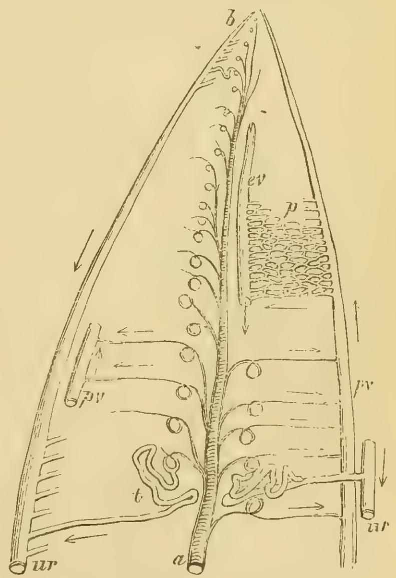
of the tuft in the parrot and in the boa, is less than in any other instance recorded; and in these animals, as is well known, the urine is almost solid. It is especially worthy of remark, that the uriniferous tubes do not exhibit a corresponding difference in dimensions.

Table of the Diameter of Malpighian Bodies, and of the Tubes emerging from them, in Fractions of an English Inch.

	Diameter of Malpighian Bodies.			Diameter of Tubes.
	Maximum.	Mean.	Minimum.	
Man	$\frac{1}{80}$	$\frac{1}{104}$	$\frac{1}{144}$	$\frac{1}{480}$
Dog	$\frac{1}{120}$	$\frac{1}{135}$	$\frac{1}{156}$	$\frac{1}{600}$
Rat	$\frac{1}{203}$	$\frac{1}{180}$	$\frac{1}{150}$	$\frac{1}{416}$
Horse	$\frac{1}{55}$	$\frac{1}{70}$	$\frac{1}{90}$	$\frac{1}{416}$
Parrot	—	$\frac{1}{430}$	—	$\frac{1}{600}$ to $\frac{1}{700}$
Tortoise	—	$\frac{1}{240}$	—	$\frac{1}{480}$
Boa	$\frac{1}{220}$	$\frac{1}{400}$	$\frac{1}{450}$	$\frac{1}{540}$

The small efferent vessel from the Malpighian tuft passes at once into the plexus round the tubes, and, as it lies between the capillary plexus of the tuft, on the one hand, and that surrounding the tubes upon the other, it bears the same relation to these two capillary systems as the portal vein bears to those of the intestinal canal and the liver; hence these efferent vessels may be regarded as analogous to a portal system of vessels. This view is further strengthened by an examination of the arrangement of the vessels in the kidney of the boa constrictor, figs. 239, 240. In this animal, the blood, after passing through

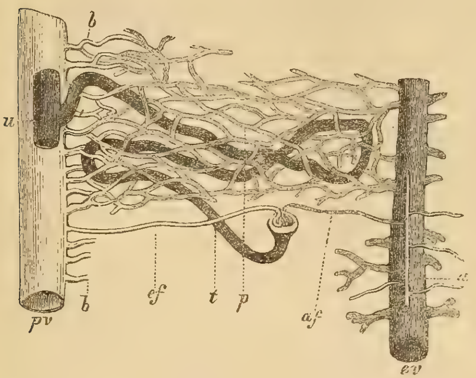
Fig. 239.



Plan of the arrangement of the elements of a lobe of the kidney in the boa constrictor. The references are the same as in fig. 240.

the capillaries of the Malpighian tuft, enters the efferent vessel, which conducts it into the branch of a portal vein ramifying upon the surface of the lobule. From the portal vein, it passes into a system of venous capillaries surrounding the tubes, from which it is at last carried into the emulgent veins, which, with the artery, lie in the central part of the lobule.

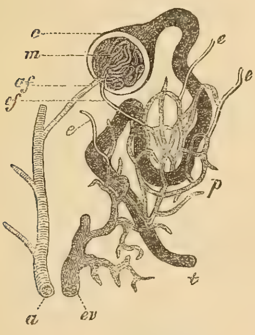
Fig. 240.



Part of fig. 239 shaded, showing the arrangement of the vessels and uriniferous tubes in the kidney of the boa, and in animals furnished with a portal vein from an extraneous source. *a.* Artery. *a f.* Terminal twig going to Malpighian body. *e f.* Efferent vessel of the Malpighian body emptying itself into a branch of the portal vein, *p v*, on the surface of the lobe. *b b.* Ultimate branches of the portal vein entering the capillary plexus, *p*, surrounding the uriniferous tube, *t*. *u.* Branch of the ureter on the surface of the lobe. *e v.* Emulgent vein within the lobe, receiving the blood from the plexus surrounding the uriniferous tubes. Supposed to be magnified about 40 diameters.

"The comparison between the hepatic and the renal portal circulation may be thus drawn in more general terms. The portal system of the liver has a double source, one extraneous, the other in the organ itself; so the portal system of the kidney, in the lower tribes, has a two-fold origin, one extraneous, the other in the organ itself. In both cases, the extraneous source is the principal one, and the artery furnishing the internal source is very small. But in the kidney of the higher tribes, the portal system has only one internal source, and the artery supplying it is proportionably large."*

Fig. 241.



Plan of the renal circulation in man and mammalia. *a.* Terminal branch of the artery, giving the terminal twig, *a f*, to the Malpighian tuft, *m*, from which emerges the efferent or portal vessel, *e f* (not shaded). Other efferent vessels, *e*, *e*, *e*, are seen entering the plexus of capillaries surrounding the uriniferous tube, *t*. From this plexus the emulgent vein (*e v*) springs.

Of the Secretion of Urine.—Having passed in review the anatomical arrangement of the different structures composing the kidney, we shall now proceed to consider briefly the functions which the several parts perform. First, with regard to the Malpighian tufts; we have already seen that in animals, in which the urinary excrement is passed in an almost solid form, the tufts are

* Phil. Trans., 1842.

small and simple compared with those in the kidneys of animals which pass the urinary constituents in solution in a large quantity of water. There can be little doubt that the special function of the vessels of the tuft is, to furnish the fluid portion of the urine while the solid matter, composed of various organic constituents and inorganic salts, is separated by the aid of the glandular epithelium which lines the convoluted portion of the tubes. "It would, indeed, be difficult to conceive a disposition of parts more calculated to favour the escape of water from the blood than that of the Malpighian body. A large artery breaks up in a very direct manner into a number of minute branches, each of which suddenly opens into an assemblage of vessels of far greater aggregate capacity than itself, and from which there is but one narrow exit. Hence must arise a very abrupt retardation in the velocity of the current of blood. The vessels in which this delay occurs are uncovered by any structure. They lie bare in a cell from which there is but one outlet."* The arrangement of the convoluted portion of the tubes is very similar to that of other secreting tubular gland-structures. We have a delicate basement membrane in contact with vessels upon one surface and having secreting epithelium upon the other. The capillary net-work surrounding the uriniferous tubes is the counterpart of that investing the tubes of the testes; and the epithelium is allied in structure to the best marked examples of glandular epithelium, and there can be no doubt that the function of these cells is such as we have described. There is no reason for supposing that the cells of epithelium undergo rapid decay and renovation; it appears more probable that they are not being constantly shed, either in an entire or disintegrated state, but that they have the power of selecting certain materials from the blood, and afterwards giving them up without their destruction. In the straight portion of the tubes the epithelium becomes thinner, and approaches more nearly to the pavement variety. It probably serves principally as a protective covering, and takes no part whatever in the secretion of the urine.

* Phil. Trans., 1842.

URINE.

Healthy urine is a clear, limpid fluid, of a pale straw colour, emitting a peculiar and characteristic odour while warm, and exciting a saline and somewhat bitter taste. As the solid constituents of this fluid are entirely excrementitious, and in great part derived from the disintegration of the tissues concerned in the chemical changes connected with animal life, we should be led to expect, that any alteration in the activity of these functions would lead to a corresponding variation in the characters of the urine. Even in a state of health the qualities of the urine vary much; and it has been found that active exercise exerts a considerable influence upon the quantity of some of the most important constituents of this fluid. Nitrogenous matter, taken in greater quantity than is required for the wants of the system, will be eliminated by the kidneys in the form of urea, and the composition of the urine will therefore be influenced by the character, as well as by the quantity, of the food.* If an unusual quantity of water be taken into the stomach, a great proportion will rapidly be eliminated by the kidneys, and the urine will be found to be very dilute, and of low specific gravity. Again, as the action of the kidneys is materially affected by the activity with which the functions of the skin are discharged, the condition of this great secreting surface has much to do with the quantity and quality of the urinary secretion. Changes of temperature, for the same reason, will cause the urine to vary in quantity. In hot weather, when the functions of the skin are increased, and a large amount of water is in this way removed from the system, in order to compensate for the effects of the increased external heat, the urinary secretion is much diminished in quantity, and becomes more concentrated, while, in cold weather, when this cooling effect of evaporation is not required, we find the amount of urine much increased, and, therefore, diminished in density. A dry, or humid state of the atmosphere, in consequence of affecting the rapidity of cutaneous transpiration, will exert a certain amount of influence on the quantity of water. It does not appear, however, that the quantity of the solid constituents excreted in a given time is much altered by these circumstances. The state of the nervous system will often be found to have a decided influence in modifying the characters of this secretion ; and various mental emo-

---

* The frequency with which we meet with an excess of urea in the urine of our countrymen is probably dependent in some measure upon the highly nitrogenous nature of our food. On the continent of Europe this is so rare, that some foreign observers appear hardly to credit the statements with reference to the frequent presence of excess of urea.

tions, such as sudden joy, or fright, or anxiety, will cause the secretion of urine having a much larger proportion of water than usual.

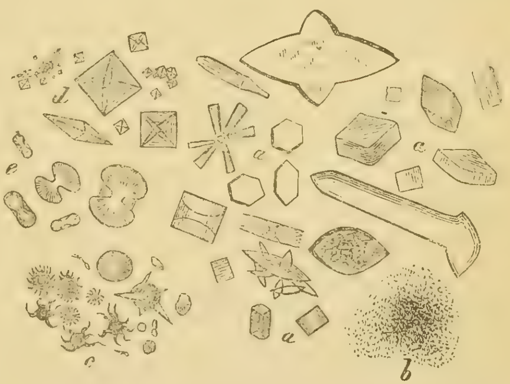
All these circumstances, and many others of less importance, have been found to affect the characters of healthy urine; and, on this account, considerable difficulty has been felt in attempting to define the precise characters of the secretion in health. Again, the composition of the urine differs at different periods of life, but in a much less degree in different individuals at the same period. The urine of men, in the prime of life, contains more solid matter, and less water, than that of old men, women, or children.

Quantity of Urine.—The quantity of urine discharged in the course of twenty-four hours, in a state of health, varies very much, but it may be said to amount to about 30 or 40 ounces. The density varies from 1·010 to 1·020 or 1·025 and the quantity of solid matter from 4 or 5 to 8 per cent. The amount of solid matter eliminated from the kidneys of a healthy man who lives well may be roughly stated to be about 1000 grains in twenty-four hours.

Reaction.—Healthy urine exhibits an acid re-action; but the intensity of the re-action varies at certain periods of the day. Dr. Bence Jones, who has lately investigated this subject, found that the urine was most acid immediately before meals, and the intensity of the acidity diminishes until five or six hours after the meal. This condition, occurring in the urine secreted soon after digestion, depends upon the quantity of alkali set free in the blood in consequence of the decomposition of certain salts which furnish the acid entering into the composition of the gastric juice.

The re-action of healthy urine has been attributed to the presence of free lactic acid, and also to acetic acid; but the investigations of Liebig have rendered it probable that it depends, not upon the existence of free or uncombined acid, but upon the presence of certain salts which exhibit a decidedly acid re-action, although there is no free or uncombined acid. Such salts are presented to us in the phosphates, which have the property of being very readily changed from the alkaline to the acid, or super-salt.

Fig. 242.



a. Various forms of lithic acid crystals. *b.* Deposit of lithate of soda, amorphous. *c.* Lithate of soda forming spherules with irregular crystals projecting from them. *d.* Oxalate of lime. *e.* Dumb-bell crystals of oxalate or oxalurate of lime.

After standing for some hours, healthy urine deposits a slight precipitate, forming a light flocculent cloud, consisting of vesical mucus, and a little epithelial debris. This deposit is much more abundant in the urine of women, in consequence of the admixture of a considerable quantity of vaginal epithelium. Not unfrequently, epithelium from the urethra, or bladder, will be found in

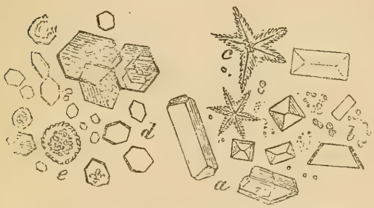
this deposit, and spermatozoa are occasionally met with. In disease, the deposit may consist of pus, or blood corpuscules, and fibrinous moulds of the

Fig. 243.

Casts of the uriniferous tubes. *a.* Casts with epithelium, at x a free cell of epithelium. *b.* Very large cast containing epithelium. *c.* Small granular casts. *d.* Small waxy cast. *e.* Casts containing fat cells and free oil at x cell filled with fat globules. *f.* Pus globules, at x one acted upon by acetic acid.

uriniferous tubes,* entangling cells of renal epithelium, which may contain many oil globules, and crystals of oxalate of lime, pus, or blood globules, are sometimes found. In such cases, the urine will also contain albumen. Among the deposits most frequently observed, may be mentioned the amorphous deposit of lithate of soda, crystals of lithic acid, of oxalate of lime, of triple or ammoniaco-magnesian phosphate, and occasionally crystals of cystine.

Fig. 244.



a. Crystals of triple phosphate. *c.* Stellate variety. *b.* Granules of phosphate of lime. *d.* Crystals of Cystine.

Composition of healthy Urine.—The urine is a highly complex fluid, and contains substances having very different properties. Its constituents are composed partly of organic, and partly of inorganic compounds which are held in solution in the aqueous portion of the secretion. A small quantity of carbonic acid gas is likewise often found held in solution. The chief organic constituents of healthy urine are the following: *urea, uric* or *lithic acid,* and certain *extractive matters,* with small quantities of *creatine, creatinine, hippuric* and *lactic acids,* and *ammoniacal salts.* The inorganic constituents consist of certain salts which enter into the composition of the food, but

* Diseases of the Kidney, by George Johnson, M.D.

which are not required for the wants of the system, and salts which, having performed certain offices by their passage through the tissues, are no longer required, and certain other saline compounds, which, like many of the organic constituents, are formed by oxidation in the processes concerned in nutrition. The inorganic salts are composed of *chlorides*, *sulphates*, and *phosphates*, with traces of *silica*, and the bases entering into the composition of these salts are, *potash*, *soda*, *lime*, and *magnesia*. It is exceedingly difficult to ascertain the precise composition of the salts as they were originally held in solution in the urine; for, in the processes of evaporation, and subsequent incineration, certain decompositions take place, which entirely alter their nature. The quantities in which these substances occur, vary in different specimens of urine, and the published analyses of the secretion in a healthy state, will be found to differ considerably from each other. This difference arises chiefly from the variation in the proportion of water; for, by calculating the relation existing between the quantities of the several solid constituents, it will be found to be nearly the same in all.

The following is an analysis of healthy human urine, by Dr. Miller. The per-centage composition of the solid matter is shown in a separate column. Specific gravity, 1·020:—

			In 100 of Solid matter.
Water		956·80	
Solid matter		42·98	
Organic matters 29·822	Urea	14·23	33·10
	Uric acid	·37	·86
	Alcohol extractive	12·53	29·15
	Water extractive	1·60	3·72
	Vesical mucus	·17	·39
	Muriate of ammonia	·91	2·11
Fixed Salts 13·158	Chloride of Sodium	7·22	16·79
	Phosphoric acid	2·12	4·93
	Sulphuric acid	1·70	3·95
	Lime	·21	·48
	Magnesia	·12	·27
	Potash	1·93	4·40
	Soda	·05	·11
		999·96	

Urea ($C_2H_4N_2O_2$) constitutes nearly half of the solid matter of healthy urine, and the secretion itself contains from 2·5 to 3·2 per cent. of this substance. The quantity, however, is much increased by exercise, or by a purely animal diet. According to Lehmann, when a highly nitrogenous diet is taken, a quantity of urea equal to nearly five-sixths of the nitrogenous matter introduced is eliminated by the kidneys. A considerable quantity of urea, however, is formed when no food whatever is taken, or when a non-nitrogenous diet is adhered to for a considerable period, which clearly shows that a large proportion of urea is derived from the disintegration of the tissues, by the process of secondary assimilation. It is often detected in abnormal quantity in the urine of patients suffering from rheumatism, and certain febrile complaints, and, in various diseases, it may sometimes be obtained from this fluid in very large quantities. This condition is very commonly associated

with diseases of the kidneys, and leads to the developement of coma, which is often fatal. Urea has been detected in the blood of patients suffering from cholera, and once by Dr. Garrod, in that of a gouty patient. In the serous fluids poured out in various parts of the body, in cases of kidney disease, as well as in several of the secretions, such as the saliva, &c., it has been found in large quantity. Dr. Owen Rees has met with it in milk, and the same observer, and Wöhler, have found it in the liquor amnii, an observation, however, which others have failed to confirm. It has been detected in the aqueous and vitreous humours of the eye.

There can be little doubt that urea is formed in the blood by the action of oxygen upon lithic acid, creatine, and, possibly, upon some of the matters comprehended under the indefinite term of extractive matter. In a state of health it is so rapidly separated from the circulating fluid, in its passage through the kidneys, that its presence is not easily recognized; but, in animals in which these organs have been extirpated, it accumulates in sufficient quantity in the blood to be detected with facility. Urea cannot be extracted from the muscles, although it is probable that the greater quantity excreted is formed from the effete materials produced by muscular action, since the quantity of urea is so much increased by exercise, and is also produced, although only non-nitrogenous food be taken. At the same time, it is almost certain, that if an amount of nitrogenous food greater than is required by the wants of the system, be taken, the excess becomes converted into urea, and is eliminated from the system by the kidneys.*

Uric or Lithic Acid ($C_{10} H_4 N_4 O_6$) is always present in healthy urine, and exists in the proportion of about one part in a thousand. It may very readily be obtained by the addition of a few drops of hydrochloric acid to a portion of the urine placed in a conical glass vessel. After the lapse of a few hours, the uric acid is found deposited in the form of small crystalline grains, adhering to the sides or collected at the bottom of the glass. Uric acid prepared in this manner is always highly coloured, which arises from the circumstance of its having a great affinity for the colouring matter of the urine.

Uric acid exists in healthy urine in combination with soda, and perhaps also with ammonia and lime; as these salts are only present in small quantity they are held in solution, but in the urine of patients suffering from fever, they often form an abundant deposit, which, in this country, is generally

* It has lately been advanced by Dr. Frerichs, that in cases in which the urea is prevented from being eliminated from the blood, either by the extirpation of the kidneys (as in his experiments upon animals), or in cases in which the functions of these organs have been impaired by disease (as in certain forms of Bright's kidney), this substance is resolved, whilst in the circulating blood, into carbonate of ammonia; the presence of which, according to this observer, gives rise to the coma which so frequently carries off patients in an advanced stage of renal disease. We should, however, state, that this view has not yet received confirmation from the experiments of others. That a considerable quantity of urea may be present in the blood without giving rise to any serious symptoms, we can affirm from actual experiment; but, at the same time, we consider that there is sufficient evidence to prove that the coma, in many cases of kidney disease, is dependent upon the presence of urea. We have tested the breath of a few patients suffering from this form of coma in King's College Hospital, and have also examined the blood, but have failed to demonstrate the presence of carbonate of ammonia.

known as lithate of ammonia, although Lehmann, Becquerel, and Heintz, all agree that it is composed principally of lithate of soda.

In the urine of the carnivora, uric acid is present in small quantity, but, as a general rule, it is absent from the urine of the herbivora; and, curiously enough also, it cannot be detected in the urine of the omnivorous pig. The excrement of birds, and that of serpents and other reptiles, and of many insects, contains a large quantity of alkaline urates. Guano, as is well known, is chiefly composed of lithate of ammonia.

After profuse perspiration, the quantity of uric acid has been found to be diminished in the urine; but a purely animal diet exerts but little influence upon the quantity of this substance excreted by the kidneys. It is much increased, however, in all febrile conditions of the system, and after imperfect digestion of food. In cases where the respiratory function is impaired, the amount of uric acid has been found to be abnormally increased; and insufficient exercise will produce a similar effect.

Uric acid has been detected in the blood of healthy men by Garrod, and in considerably increased proportion in the blood of gouty patients. It has also been detected in the perspiration, and the deposits formed about the joints of gouty persons are largely composed of it.

According to Wöhler and Frerichs, the introduction of lithic acid into the blood is followed by an increased secretion of urea and oxalate of lime in the urine, a point of considerable interest when we know that, by the influence of peroxide of lead, a similar decomposition of the lithic acid may be induced artificially.

When all these circumstances are considered, more especially that, in certain instances in which the respiratory changes are not carried on with the activity consistent with perfect health, a greatly increased quantity of lithic acid is eliminated by the kidneys, there appears ample evidence to show, that lithic acid is one of the purely excrementitious substances derived from the disintegration of the tissues, and formed by the action of oxygen upon effete material. By a process of further oxidation, the lithic acid itself becomes converted into urea as we just now mentioned.

Hippuric Acid ($C_{18} H_8 N O_5$, HO), according to Liebig, exists in small quantity in healthy human urine, but it is obtained in considerable quantity from the urine of horses, cows, and other herbivorous animals. It is quite inodorous, has a rather bitter taste, is slightly soluble in cold, but very soluble in hot water and alcohol, characters in which it differs from uric acid. It is easily prepared from the urine of cows by precipitation by hydrochloric acid, and subsequent purification. It is, however, absolutely necessary that the urine should be perfectly fresh, otherwise the hippuric acid will be found to have been entirely converted into benzoic acid, a change which may also be induced in the pure acid by the action of heat and mineral acids. It has been stated by Mr. Ure, that if benzoic acid be taken, it is eliminated from the system as hippuric acid.

Hippuric acid has been found in the urine of many herbivorous animals, and by Lehmann in that of the tortoise (*Testudo Græca*) and many herbivorous insects. It is not present in the urine of the carnivora. In cases of diabetes, it is stated by the same observer to be never absent from the urine; and in health may usually be detected if the diet be purely of a vegetable character. This acid, like uric acid, must be looked upon as an excrementitious substance, and plays no other part in the system.

Creatine ($C_8 H_9 N_3 O_4$) occurs in very small quantity in the urine. It is a colourless crystalline body, with a strong pungent taste, soluble in cold and very soluble in boiling water; it is almost insoluble in alcohol. Boiled with baryta water, it becomes changed into urea and sarcosine; and it is probable that a somewhat similar decomposition ensues within the organism, and that of the quantity of creatine formed in the muscular fibre a large proportion is eliminated from the system in the form of urea, and partly perhaps as carbonic acid and ammonia.

Creatine was obtained in the beautiful investigation of Liebig from the flesh of various animals; but the proportion in which it exists is so small, that it can only be extracted with great care, and by operating upon large quantities. It occurs most abundantly in the flesh of fowls, and in the heart of the ox.

Creatinine ($C_8 H_7 N_3 O_2$) is also met with in the urine, and its presence in this fluid was discovered by Liebig, to whom we are indebted for all that is known in reference to this body. Creatinine crystallises in colourless crystals. It possesses a hot burning taste, compared to caustic ammonia. It is soluble in water, and, unlike creatine, is freely dissolved by spirit. It is found with the last-mentioned body in the juice of muscular fibre. Creatinine may be formed by the action of hydrochloric acid upon creatine, a change which renders it probable that it is also formed from the last named body in the organism. In urine, creatinine exists in larger quantity than creatine; while in muscular fibre the latter is found to exceed the former in amount.

Extractive Matters.—Under this very unsatisfactory term are included certain substances met with in the urine, blood, and other animal fluids, which are not easily isolated, whose properties are with great difficulty determined, which do not crystallize, are not volatile without decomposition, and cannot be obtained in a pure form. Of late years, however, several substances have been separated from the extractive matters which were formerly included under that term. Of these, albuminate of soda, creatine, and creatinine may be referred to as examples. These extractive matters no doubt play a most important part in vital chemistry, and probably represent a stage intermediate between the nutritive pabulum and the tissues formed from it, or between the latter in process of disintegration and the compounds we have been considering, such as urea, lithic acid, etc., but in the present state of our knowledge, little beyond mere speculation can be advanced.

Our friend, Dr. G. O. Rees, found that, in cases of albuminuria connected with kidney disease, large quantities of the extractive matters of the blood passed off in the urine as well as albumen. The test which Dr. Rees employed for detecting the presence of the blood-extraction was the tincture of galls.*

Ammoniacal Salts.—Ammonia exists in very small quantity, if indeed it be present in healthy urine, but in disease a considerable proportion may occur. It has been found as hydrochlorate, lactate, biphosphate, ammonio-magnesian or triple phosphate, and in the form of phosphate of ammonia and soda. Its presence usually depends upon the decomposition of some of the nitrogenous constituents of the urine, as previously indicated.

Fixed Salts.—By the careful incineration of urine we obtain the fixed salts, and we find that, of the saline residue, part is soluble and part insoluble in

* Lettsomian Lectures. London Medical Gazette, vol. xlviii. 1851.

water; the latter having been previously held in solution in the urine by some material which has been destroyed by a red heat. Although the presence of certain acids and certain bases in the ash is readily demonstrated, the precise manner in which these were originally united together is not so easily ascertained.

The most important saline constituents of normal urine are chlorides, sulphates, and phosphates; and the following bases are present, potash, soda, lime, magnesia, with traces of silica and peroxide of iron.

Chlorides.—The chlorine exists in combination with sodium, in the form of common salt, and perhaps also occasionally as hydrochlorate of ammonia. Almost the whole of the chloride of sodium is probably derived from the food; although, from recent investigations, it appears probable that this substance plays an important part in the development of tissues, and also in certain morbid changes. In growing tissues, it is always abundant, and in the fluid on the surface of healing ulcers it exists in large quantity.*

Sulphates.—The sulphuric acid exists in combination with potash, and perhaps also with soda. The sulphates are highly important saline constituents, and their proportion is much influenced by the activity of the vital functions, and also by an animal diet. After exercise, the amount of the sulphates, as well as that of the urea, undergoes an increase; and it has been found, that in *Chorea* (a disease characterized by inordinate action of the muscular system) a large quantity of these salts are excreted in the urine.† The sulphuric acid is, doubtless, in great measure produced by the oxidation of the sulphur contained in the proteine compounds. Unlike the chlorides, the sulphates are not present, or are only met with in very small quantities, in the fluids of the body generally, with the exception of the urine, a circumstance which points to the importance of the former in the organism, while it clearly shows that the latter are not required in the nutritive changes, and are, therefore, only to be found in the excrements.

Sulphuretted Hydrogen is from time to time detected in urine. Dr. Beale met with it frequently in the urine of insane patients. Sulphur is no doubt eliminated in considerable quantity in the urine in certain cases. Cystine contains as much as 26 per cent. of this substance.

Phosphates.—Phosphoric acid is found in combination with soda, lime, and magnesia; the salts thus constituted have been spoken of as alkaline or earthy phosphates, the former term being confined to the combination of phosphoric acid with soda, and the latter to the phosphates of lime and magnesia, which are precipitated from healthy urine by the simple addition of excess of ammonia.

The large amount of phosphates present in urine is chiefly derived from the food, but part results from the oxidation of the phosphorus which is contained in the tissues; the particular tissue concerned in the formation of this phosphoric acid being the nervous, which, it is well known, contains a large proportion of phosphorus. Dr. Bence Jones found an increase in the quantity of the alkaline phosphates in the urine of some cases of inflammation of the brain, and a diminution in quantity in cases of delirium tremens when no food was taken; but in the latter case the diminution is, probably,

* "On the Diminution of the Chlorides in the Urine in Cases of Pneumonia," by Lionel Beale. Med. Chir. Trans., vol. xxx.

† Dr. Bence Jones. Med. Chir. Trans.,

too slight to be recognised. This circumstance would account for the result of several experiments we have ourselves made upon this point, in which we have found no diminution in the quantity of phosphates.

To sum up, the kidneys appear to be special organs for the removal of effete material produced in the vital processes from the system, and they serve as channels for the elimination of water and certain saline matter, as well as excess of nitrogenous material which is not required for the maintenance of the tissues. The chief constituents of the urine consist of compounds resulting from the action of oxygen upon the albuminous or allied substances; and in urea and uric acid we have probably examples of the highest state of oxidation which the chemical elements of the tissues are capable of undergoing, and urea may be looked upon as the last of a series of compounds resulting from the successive action of oxygen upon those bodies which stand above it on this scale. The fixed salts which occur in urine also exist in a highly oxidized state. There can be little doubt, that the highly complex substances entering into the formation of the tissues, by chemical action taking place in the organism, become resolved into bodies of a more simple composition, until they are eliminated in the form of urea or some allied compound, the elements of which are so loosely combined, that by external circumstances alone new substances are formed of a still simpler composition, such as carbonic acid and ammonia. In these, however, the elements are united with such force, that it is only by most powerful chemical action, or by the still more powerful influence of the vital properties of plants, that they can be separated from each other, and again applied to the building up of those highly complicated substances of which the tissues of animals consist, and which, by their vital processes, are again reduced in complexity as before.

The more actively the vital phenomena are performed, or, in other words, the greater the rapidity with which the disintegration and repair of the tissues takes place, the larger is the quantity of urea excreted from the system. With this increase of the urea, there is certainly a corresponding increase of the sulphates, and perhaps also of the phosphates. If, however, the activity of these changes be interfered with, as from impairment of the respiratory apparatus, or from other causes, as might be expected, we find an increase of that constituent which stands next above urea in the descending series of compounds resulting from oxidation, namely, *lithic acid.* This finds its way out of the system in the form of lithate of soda, forming the amorphous sediment generally known as lithate of ammonia, but which really consists almost entirely of lithate of soda. Under similar circumstances, we often meet with a deposit of *oxalate of lime.* The urine of the active carnivora contains, like that of man, a large quantity of *urea;* on the other hand, the urine of serpents and many other reptiles consists almost entirely of *uric acid* in combination with ammonia. The urine of birds much resembles in character that of serpents, which appears somewhat to be opposed to the doctrine we have been endeavouring to inculcate, as the vital changes are carried on with greater activity in this than in any other class of animals; but, on the other hand, it may be argued, that the demand for oxygen is so great in birds, and their vital functions so actively carried on, that the extensive respiratory apparatus necessary for the supply of sufficient oxygen to convert all the uric acid into urea would be incompatible with the lightness of their bodies, which is so necessary for flight; while the removal of the

urinary constituents in a state of solution involves the necessity of a bladder, or receptacle, in which it can collect, and which would still further add to the weight. We find in the minute anatomy of the bird's lung a beautiful arrangement by means of which not the smallest space where blood can be exposed to the action of air is lost. (Vide p. 395.)

Pelvis of Kidney and Ureters.—The mucous membrane lining the pelvis of the kidney is continuous with that of the renal tubes at the point where they open upon the papillæ, in which situation it is exceedingly thin, and it is difficult to distinguish its epithelium. The epithelium of the pelvis of the kidney generally is polygonal in form, and constitutes a tolerably thick layer. The deeper cells are small and rounded. Many cells approaching to the columnar form may also be observed; and these increase in number towards the ureter, which tube is lined with this variety of epithelium.

The ureters have muscular coat composed of two layers, an internal layer of circular, and an external one of longitudinal fibres. These are prolonged upwards into the pelvis of the kidney, and cease at the calyces. The muscular coat is composed entirely of unstriped muscular fibre cells, the nature of which will be particularly described when we come to speak of the uterus, and it is invested with an external coat composed of fibrous tissue.

The ureters reach the base of the bladder, run obliquely through its coats for the distance of nearly an inch, and open into this viscus by two narrow slit-like openings about an inch and a half behind the prostate on its inferior surface, and separated from each other by the distance of nearly two inches. The openings readily permit the urine to pass into the bladder; but, by their arrangement, completely prevent its reflux into the ureter; the reflexion of mucous membrane at their mouth serves the office of a valve.

We have already referred to the contraction of the ureters in p. 457 of the present volume.

Bladder.—The urinary bladder is the large receptacle into which the urine is poured and in which it accumulates as it escapes from the ureters. Its size varies very greatly: it may be distended to such a degree as to contain nine, or even twelve pints of urine, in which case its walls of course become exceedingly thin, or it may be contracted so much as to leave scarcely any visible cavity in its interior. Its contracted muscular walls may be found half an inch or more in thickness, a condition very often met with in cases of cholera.

The internal surface of the bladder has a reticulated appearance,

owing to the arrangement of the muscular fasciculi. The mucous membrane is sometimes forced through the small spaces between the fibres, and thus a number of sacculi are produced, a condition termed *sacculated bladder*.

At the lower part of the bladder is a perfectly smooth and pale surface, of the form of an equilateral triangle, the apex of which points towards the prostate. The ureters open one at each of the posterior angles; and between them there is a prominent line caused by the mucous membrane being somewhat raised in this situation. This triangular portion of the floor of the bladder is called the *trigone* (triangle), and the mucous membrane is attached more firmly than in other parts to the muscular coat beneath, whence its smooth character. The bladder is only partially covered with peritoneum. It is connected in the male with the rectum, and in the female with the uterus and upper part of the vagina by much loose areolar tissue, which permits great freedom of movement of these parts upon one another.

The bladder is kept in its position by certain reflexions of peritoneum passing over bands of white fibrous tissue, or *reflexions of the vesical fascia* (*true ligaments*), and by folds of peritoneum alone (*false ligaments*).

The anterior reflexions of the vesical fascia constitute the *anterior true ligaments of the bladder*. These arise from the lower margin of the pubis on each side of the symphysis. They then pass over the upper surface of the bladder. Many of these fibres are attached to the muscular fibres, and this ligament may be said to serve as the tendon of attachment of many of the fibres which constitute the detrusor urinæ muscle.

The fundus of the bladder is connected with the umbilicus by the suspensory ligament of the bladder, a reflexion of peritoneum which encloses the obliterated hypogastric arteries and urachus.

The muscular coat of the bladder is composed entirely of unstriped fibre-cells, which are much interwoven, but may be described as arranged in two layers, an external longitudinal, and an internal transverse or circular.

The latter are exceedingly numerous round the neck of the bladder, whence they have received the name of Sphincter Vesicæ.

The longitudinal fibres are most abundant upon the anterior and posterior surfaces of the bladder, and constitute the *detrusor urinæ* muscle.

The *mucous membrane* is of a pale colour, and is loosely con-

nected to the muscular tissue by the intervention of much loose areolar tissue, in which the yellow element is abundant, except over the trigone, where it adheres very firmly, by which a perfectly smooth surface is produced in this situation.

About the neck of the bladder are a number of small glands, each consisting of a few secreting follicles, opening into a short wide duct. These are lined with columnar epithelium, and secrete a perfectly clear transparent mucus.

Epithelium.—The epithelium of the bladder varies much in its character in different situations. Near the orifices of the ureters it is almost entirely of a columnar form; but over the fundus, generally, it consists of large circular and oval cells, with a distinct nucleus. These are of very large size, and present a very characteristic appearance. Kölliker describes many of these large cells as lying upon the surface of columnar epithelium, their deep aspect being hollowed out to receive the summits of the latter cells. Towards the urethra, the columnar epithelium again predominates. Epithelium from various parts of the mucous membrane above referred to is often found in the urine; and the characters are often so distinctive as to enable the observer to infer with accuracy the locality from whence it was derived, a point which is occasionally of some value in diagnosis.

We shall consider the anatomy of the urethra, and other organs connected with the bladder, in the chapter on the *Organs of Generation.*

The student should consult the following works and monographs for more detailed information upon the subjects treated of in the present chapter: M. Malpighi, de Renibus, 1669; Schumlansky, de Structurâ renum, 1788; W. Bowman, in the Philosophical Transactions for 1842; Goodsir, in the Monthly Journal of Medical Science, 1842; Dr. Johnson's article, "Ren," in the Cyclopædia of Anatomy and Physiology, and his work on Diseases of the Kidney; and the treatises on Physiology and Minute Anatomy before referred to.

Upon the Urine. — Dr. Golding Bird, on Urinary Deposits; Dr. Bence Jones' Lectures upon Animal Chemistry; Lehmann's Handbuch der Physiologischen Chemie, Leipzig, 1854; translated by the Cavendish Society. J. E. Bowman, Medical Chemisty. Beale, on the Microscope, and its application to Clinical Medicine, Chapter XIV.

CHAPTER XXXV.

ON THE DUCTLESS GLANDS.—SPLEEN.—ITS CAPSULE.—TRABECULAR TISSUE.—SPLEEN PULP.—SPLENIC ARTERY.—MALPIGHIAN CORPUSCLES.—VEINS OF THE SPLEEN.—LYMPHATICS.—NERVES.—CHANGES IN THE BLOOD IN THE SPLEEN.—USES OF THE SPLEEN.—SUPRA-RENAL CAPSULES.—THYROID BODY.—USES OF THE THYROID.—THYMUS.—USES OF THE THYMUS.

We have now to consider a remarkable class of organs present in all the mammalia, which resemble the secretory glands already described in external conformation and in the possession of a solid parenchyma, but differ from them in the absence of any excretory apparatus suitable for carrying off the products of secretion. These organs cannot be associated with such structures as the liver, the kidneys, and the other glands; inasmuch as they not only differ from them in the essential particular just mentioned; but they exhibit in their internal structure no mechanical arrangement clearly adapted to a secretory function; nor is any material (save in the case of the thymus) to be obtained from them bearing any resemblance to a secreted product. Many physiologists, however, suppose that these organs do exert an attractive influence on certain matters in the blood, and separate them from it; but this hypothesis necessarily involves a second and a less plausible one, that the matter thus extracted must re-enter the circulation.

These bodies agree in the common characteristic, that their parenchymatous portion consists of cells and cell-nuclei, with blood-vessels in great number variously disposed. They may probably be regarded as appendages to the vascular system, and, from the absence of any excretory duct, they are usually designated *vascular ductless glands*: under this head are grouped—the spleen, the supra-renal capsules, the thyroid body and the thymus.

Spleen.—The spleen is of an oval form and somewhat compressed;

its internal surface is concave, and its external surface is in contact with the diaphragm. The spleen lies in the left hypochondrium, and extends upwards as high as the tenth rib, but when enlarged reaches much higher, and increases upon the lower part of the thoracic cavity. The spleen is of a dark red colour, highly vascular, and of a soft pulpy consistence; it varies much in size, according to the state of general nutrition, and also at different periods of the digestive process. The weight of the spleen compared to that of the body at birth, is as 1:350, in adult life 1:320, and in old age as 1:700. The following points have to be noticed in considering the structure of the spleen: the capsule, the trabecular tissue, the spleen pulp, or proper splenic parenchyma, and the arrangement of the arteries, veins, nerves, and lymphatics.

Capsule of the Spleen.—The spleen is covered by a reflexion of peritoneum, which extends to it from the fundus of the stomach, and is called the gastrosplenic omentum. The proper capsule of the spleen is composed of white and yellow fibrous tissue, and permits of considerable distension. It envelopes the organ entirely, and is prolonged into the interior upon the vessels, which are enclosed in sheaths composed of a structure closely resembling the capsule of the organ. In man there is an absence of muscular fibre-cells in the capsule; but in the dog and pig, and some other mammalian animals, they are very numerous.

Trabecular Tissue of the Spleen.—If a section of a spleen be carefully washed under a stream of water, the dark-coloured soft pulpy matter is removed, and a perfectly white and complicated fibrous meshwork remains. The interspaces bounded by these trabeculæ vary much in size and form; but they are all intersected by still smaller trabeculæ, and these smaller spaces by fibres visible only by the aid of the microscope. The network thus formed, much resembles that of the corpora cavernosa penis, and the fibres composing it, are intimately connected with the fibrous capsule of the organ, and also with the sheaths of the vessels supplying it. The spaces or interstices communicate freely with each other, and in them is situated the pulpy tissue of the spleen.

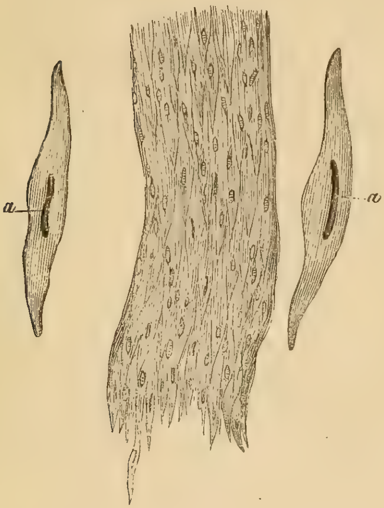
Fig. 245.

Cells from the trabecular tissue of spleen of human fœtus at full time. Magnified 215 diameters.

The larger trabeculæ, like the fibrous capsule of the organ, are composed chiefly of white fibrous tissue, with some fibres of the yellow element. The smaller trabeculæ are composed of elongated spindle-shaped cells,

about the 300th of an inch in length, and about the $\frac{1}{5000}$th of an inch broad in the centre, which is their widest part. They contain a distinct elongated or oval nucleus. The nucleus is often found bulging upon one side of the fibre cell, and in some instances appears only connected with it by a stalk. The cell is often much curved, and sometimes bent upon itself, an appearance arising from its mode of development, which takes place, according to the observations of Mr. H. Gray, by the solution of the cell wall at a point opposite the nucleus, which latter remains, and the cell wall itself forms the fibres which are prolonged from either side of it.

Fig. 246.



Muscular fibre cells from the spleen of the sheep, magnified 400 diameters. *a*, *a*. Fibres more highly magnified. After Mr. Gray.

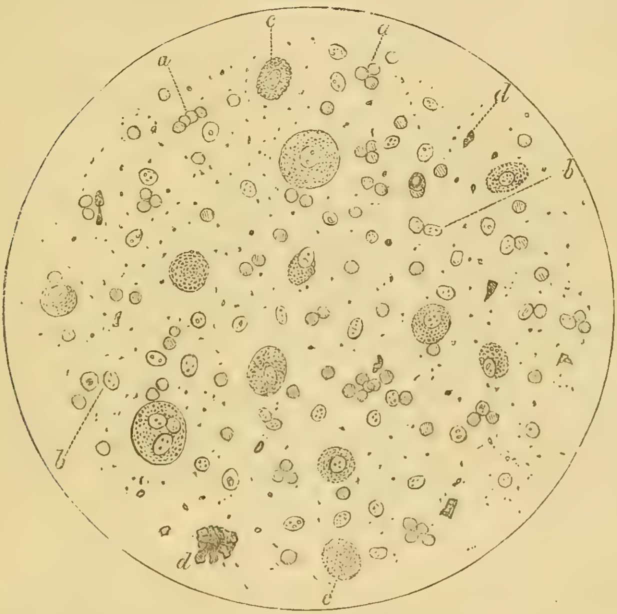
In several of the mammalia, both in the capsule and also in the trabeculæ, a number of muscular fibre cells, with a distinctly oval elongated nucleus, are present. The fibre may be entirely composed of these cells. They are not present in the human spleen, but may be readily demonstrated in that of the sheep. The spleen possesses very slight power of contractility, and in experiments upon the spleen of the ox and sheep, Mr. Gray was unable to obtain marked contractions by the application of a strong galvanic current.

Spleen Pulp.—The spleen pulp, or parenchyma, the proper tissue of the spleen, is composed of peculiar colourless cells, containing masses of colouring matter, free coloured particles, granular matter, and blood corpuscles.

The *colourless portion* of the spleen pulp is composed principally of small circular cells, or nuclei, about the size of a blood corpuscle, and having a faintly granular appearance. These small nuclei vary somewhat in size, and are interspersed with a considerable quantity of granular matter, which is often collected around them. The spleen pulp also contains a few nucleated vesicles, nearly $\frac{1}{1000}$th of an inch in diameter.

These colourless elements constitute a considerable proportion of the spleen pulp, and are in contact with the capillary walls, and with the Malpighian corpuscles of the spleen. Great variation occurs in the size and general character of the cells and nuclei which compose the colourless elements, and they vary much in quantity in different physiological conditions of the system. Mr. Gray has shown, that in well-fed animals they are much more abundant than in those supplied with an insufficient quantity of food, and their proportion increases after the completion of the digestive process.

Fig. 247.



Pulp of the human spleen. *a, a.* Blood corpuscles. *b, b.* Dotted nuclei. *c, c.* Nucleated vesicles. *d, d.* Coloured corpuscles of hæmatine. From Gray on the Spleen.

They are composed of a proteine compound, and in their chemical characters closely resemble the white corpuscles of the blood.

The red colour of the spleen pulp is due to the presence of a great number of blood globules and coloured corpuscles, free or contained within cells.

The blood globules are frequently observed to be smaller than in other situations; their outline is often indistinct; sometimes their surface appears corrugated or shrunken, and their walls in some places collapsed; their outline is irregular and angular, and in

many instances corpuscles are seen evidently breaking up into small irregular masses of red colouring matter. These appearances indicate that the red blood corpuscles are undergoing a process of disintegration, but this change also appears to be effected in another and very peculiar manner, which was first described by Kölliker. Several blood corpuscles (from one to nine or ten) collected together, appear to become covered with an investing membrane, adhering to the interior wall of which, a distinct nucleus may be observed. Such appears to be the manner in which these blood corpuscle-holding cells are formed, but whether the nucleus precedes the formation of the cell or succeeds it, is not known. The blood globules within now undergo disintegration in the manner just referred to, and at length the cell contains only coloured granules, varying in size and form. These granules gradually become of a golden yellow colour, and then paler, until at last the contents of the cell become almost decolourized.

Occasionally, red crystals are seen in the blood corpuscles of the splenic parenchyma, as was first observed by Funke; and not unfrequently numerous free coloured acicular crystals are met with.

These appear to be the most important changes which take place in the disintegration of the red blood corpuscles in the spleen pulp. In some animals, the disintegration seems to occur entirely within the large cells; while in others, the blood corpuscle-holding cells are very rarely met with, and the blood globules become broken down into coloured granules without being at any time enclosed in a cell. In other cases, again, both processes occur. In the course of very numerous observations upon the human subject, Mr. Gray only observed blood corpuscles enclosed in cells in two instances, and then in very small number.

We may observe here, that Gerlach interprets these facts in a totally different manner, and considers that the changes taking place in the blood corpuscle-holding cells occur in the reverse order to that which we have described. In fact, he considers that the blood corpuscles are *formed* in these cells, commencing as irregular yellow granules, and gradually becoming developed into the perfect red blood globule. In this view Virchow appears to coincide. Dr. Hughes Bennett, of Edinburgh, also considers the spleen as a blood-forming organ.

The changes above referred to take place in the spleen pulp which lies between the trabeculæ, and, of course, external to the capillary vessels. Now, we have to enquire how the blood corpuscles leave the vessels and enter the pulp.

Mr. Gray has shown that many of the capillary vessels are not directly continuous with the veins, but that the blood, in passing from one set of vessels to the other, traverses intercellular spaces in the spleen pulp. The veins also, in many cases, appear to commence in intercellular spaces, so that it is not difficult to conceive how the contents of the vessels extravasate into, and become mixed with, the constituents of the pulp, especially when the organ is distended with blood. These changes appear also to take place to a more limited extent within the veins themselves. Although this may be the correct explanation of the manner in which the cells in the pulp communicate with the blood in the vessels, we cannot look upon it by any means as demonstrative.

Splenic Artery.—The splenic artery is the largest branch of the cæliac axis, and the size of this vessel in proportion to the organ to

Fig. 248.

Transverse section of the human spleen, showing the mode of distribution of the arteries, and the manner in which their sheaths are formed. After Mr. H. Gray.

which it is distributed, is considerably larger than that of other glands, with the exception of the thyroid. The large size of the vessel would lead to the inference that more arterial blood is distributed to the spleen than is required for the mere purposes of nutrition. The branches of the artery are invested with sheaths derived from and continuous with the fibrous capsule of the organ, and they have a similar structure to it. Each arterial branch is distributed to a particular part of the organ, and it does not anastomose with contiguous branches. The smaller arteries, about the $\frac{1}{200}$ of an inch in diameter, are connected with the Malpighian bodies, which are usually placed in the points of bifurcation of the vessel.

Malpighian Corpuscles.—Upon making a section of a fresh ox's spleen, a number of small round whitish bodies will be seen. They are sometimes collected in groups of four or six together, and appear to be connected with the smaller arteries, which are in close proximity to them. These small bodies have been named Malpighian corpuscles from their discoverer; they are in close contact with the spleen pulp, except at the points where they are in connection with the coats of the artery.

The Malpighian corpuscles are very distinct in pigs, sheep, oxen, and guinea pigs. In most other mammalia they are to be demonstrated, although with greater difficulty. In the human subject they are constantly present; but often are not to be distinguished in consequence of rapidly undergoing post mortem change. In birds, these bodies are very numerous, and have been observed, by Müller, in the chelonia, among reptiles, but they cannot be seen in the naked amphibia. In fishes, they appear to be absent.

Fig. 249.

This figure shows the connection of a splenic corpuscle with the neighbouring vessels, according to Mr. H. Gray. The corpuscle is placed at the angle of bifurcation of one of the small arteries, its external surface being covered by a close and delicate capillary plexus, whilst its circumference is invested by a mesh of large veins, which radiate in every direction from its margins. The comparative size of the arteries and veins, the capillary plexus of the pulp, and the mode in which these vessels communicate with the veins, are shown in this figure.

The splenic corpuscles are placed upon a small branch of the arteries as upon a short peduncle or stalk, which sometimes consists only of fibrous tissue, prolonged from the sheath of the vessels, or they lie in the angle formed by the divergence of two branches from each other. The artery divides into numerous branches upon the surface of the Malpighian corpuscles. The observations of Kölliker and Dr. Sanders, which have lately been confirmed by Prof. Huxley, have shown that the substance of the corpuscle itself is traversed by small capillary blood-vessels. These small vessels probably pour their blood into small veins which surround the corpuscle, and are of considerable size. According to Mr. Gray, these veins receive the secretion of the Malpighian bodies.

The Malpighian corpuscle does not appear to us to be invested with a distinct and well-defined membranous capsule; but we are inclined to agree with Remak and Leydig, who represent their contents as not being separated by any distinct line of demarcation from the splenic pulp, although the fibrous tissue derived from the external wall of the vessels appears to form a sort of imperfect capsule. The cells of which these bodies are composed readily pass from them into the pulp. Mr. Gray has made the interesting observation, that these bodies are very large, and well defined in well-fed animals, and that, during the latter part of the digestive process, they increase in size, while, in animals insufficiently fed, they are very small, or absent altogether. In the latter, little increase is noticed in their size after digestion. Their increase is considerable under the influence of an albuminous diet; but when animals are confined to fat or gelatine, these bodies are not to be distinguished.

Veins of the Spleen.—The splenic vein is the largest branch of the vena porta, and, like the others, is destitute of valves. The branches into which the vein divides, do not communicate with each other in the substance of the organ. Mr. Gray describes three different modes in which the veins commence:—1. As continuations of the capillaries of the arteries, which is the most common method; 2. By inter-cellular spaces in the substance of the spleen pulp through which the veins communicate with each other. The smallest veins commence in this manner; or 3. By forming an imperfect capsule to each Malpighian body. This latter mode of commencement has not been described by other observers, and Mr. Gray considers these small veins as the channels by which the secretion of the Malpighian bodies is carried into the circulation.

The vein ramifies abundantly upon the surface of the spleen,

and, as it enters into the organ, receives an investment of fibrous tissue, which is prolonged upon the branches, forming their sheaths, which are connected with the trabeculæ.

Lymphatics.—But little is known of the ultimate arrangement of the lymphatics of the spleen, or of the manner in which they commence. They are certainly not connected with the Malpighian corpuscles, nor can we look upon them as the channels which carry off the secretion of the organ, a view which has been advocated by many observers.

Nerves.—The nerves of the spleen are derived from the splenic plexus formed by branches from the left semilunar ganglion, and from the right pneumo-gastric nerve. The branches are distributed to the coats of the arteries; they may be traced upon them for a considerable distance, but gradually they become lost.

Changes in the Blood in the Spleen.—The most important peculiarities in splenic blood appear to be the following:—The total quantity of solid matter is considerably less in the blood of the splenic vein than in arterial or venous blood, and the blood corpuscles are reduced to half the quantity. The greatest reduction seems to occur at the period of the greatest turgescence of the spleen. Mr. Gray has made the very interesting observation, that in starved animals no change is observable. The albumen is increased, particularly when the amount of blood corpuscles is much diminished. The quantity of fibrine in splenic blood, is also found to be increased. The serum is often observed of a pale reddish brown colour.

Uses of the Spleen.—We have now to consider the uses of the spleen in the animal economy. From the large quantity of elastic tissue in its capsule and trabeculæ, it seems eminently adapted to undergo great changes in volume; and the direct experiments of Dobson, and many other observers, have proved that it becomes much enlarged during digestion, as well as when blood was injected into the jugular vein. Connected with the large veins of the portal system, it forms a dilatable diverticulum, or reservoir, in which blood may, for a certain time, be contained, thus preventing dangerous congestion of the veins of the liver, and some other abdominal viscera, and, indeed, of the venous system generally. The spleen does not appear to be contractile. In several careful experiments, Mr. Gray was never able to cause more than a slight corrugation of the surface of the organ by the galvanic current, although active contractions could be produced in the œsophagus, or stomach, under similar circumstances. In no instance out of

twenty experiments, was blood expelled from the organ, or its diameter diminished. Not only does the spleen perform this physical office, but, as has been shown, certain important chemical and microscopical changes are found to have occurred in the blood which has passed through this organ. In 1847, Kölliker advanced the theory that blood corpuscles became disintegrated in the spleen, an opinion which was afterwards supported by Ecker and Béclard. From various facts which we have alluded to, we cannot but look upon this point as decided in the affirmative, although others have been led to adopt the view, that blood corpuscules are actually formed, instead of being disintegrated, in this organ. Kölliker thought that the colouring matter of the blood was changed in the spleen, and converted into the peculiar colouring matter of the bile; but Mr. Gray has shown, that yellowish-green bile is found in the gall-bladder of the chick, at a period considerably antecedent to the development of the splenic vein. The small size of the spleen in the fœtus, as compared with its increase after birth, and in adult life, renders it improbable that in intra-uterine life it acts the part either of a blood-forming, or blood-destroying, organ.

Its great increase in size, in well-fed animals, and its diminution in insufficiently-fed animals, and, especially its increase after the completion of digestion, render it extremely probable that it has the power of storing up albuminous material for future consumption, when a larger quantity of nutrient material is taken than is required for the immediate wants of the system. The cells of the Malpighian corpuscles appear, from Mr. Gray's observations, to be the organs especially concerned in this process.

Supra-renal Capsules.—The supra-renal capsules are two bodies of a somewhat triangular form, situated one on each side of the spine, a little above the corresponding kidney, to the capsule of which each is connected by loose cellular tissue.

Each supra-renal capsule is about an inch and a half in depth, somewhat less in width, and usually about half an inch in thickness. The weight varies from one to two drachms. The gland is enclosed in a thin fibrous capsule, which dips down into its substance. It is surrounded with loose areolar tissue, containing an abundant quantity of fat.

Upon making a section through the body, it is found to be composed of two distinct portions, a *cortical* and a *medullary part.* The former is of a yellowish colour, shading into a brown border towards the interior. It tears somewhat readily, and then exhibits

a fibrous appearance. The medullary substance is of a paler color, unless the vessels are injected with blood, and of a somewhat softer consistence. If the gland be not perfectly fresh, a cavity is usually seen in the interior, which results from the breaking down of the medullary tissue.

The cortex is divided into a series of compartments or tubes by septa of fibrous tissue prolonged inwards from the capsule of the organ. These spaces extend through the entire thickness of this part of the body, and pass from the surface vertically inwards. They contain numerous oval or spherical bodies, varying considerably in length. These have been looked upon by Ecker as gland-follicles, but Kölliker considers them merely as aggregations of cells not invested with a distinct membrane, or enclosed in a larger cell. They are separated from each other by meshes of areolar tissue, the fibres of which often appear to be connected with the surface of the mass. In the outer part of the cortex separate cells, filled with pigment granules, are usually to be met with; but in the inner portion, round or oval vesicles are found, which are filled with oil globules.

The medullary substance is composed of a network of areolar tissue which is prolonged from the cortex, and contains numerous vessels, in the meshes of which are found many cells, some of which contain fat or granular pigmentary matter. A distinct nucleus and commonly a nucleolus are seen, and often the cells have many angular processes, or are much branched; indeed, these cells present an appearance much resembling that of the nerve vesicle.

Besides the fibrous, vascular, and cellular, elements just described, the medullary portion of the supra-renal bodies is very largely supplied with nerve fibres derived from the semilunar ganglia and solar plexus, with a few fibres also from the pneumo-gastric, and from the phrenic. The nerves appear to perforate the cortical substance in several places, pass through this, and enter the medullary, where they form a plexus amongst the fibrous tissue. The mode of their termination has not been made out.

The function of these peculiar bodies is entirely unknown. From the great dissimilarity of structure observed in the cortical and medullary portions of the organs, it is probable that each performs a distinct and separate office. In the present state of our knowledge we may continue to classify the former with the ductless or vascular glands, but, from the existence of cells much resembling nerve vesicles, and an abundant plexus of nerve fibres, it appears more correct to regard the latter as connected in some man-

ner with the nervous system, and probably with the sympathetic. Bergman thinks that this part of the supra-renal body may, perhaps, bear a relation to the sympathetic, similar to that which the pituitary body does to the brain. It is interesting to note, in connection with this subject, that our friend, Mr. Brown-Séquard, has observed congestion, and hypertrophy of the supra-renal capsules, after injuries to the chord in the dorsal region.

Dr. Addison has lately published an account of several very interesting cases of disease of the supra-renal capsules, associated with "anæmic general languor and debility, remarkable feebleness of heart's action, irritability of the stomach, and a peculiar change of colour in the skin."*

Thyroid.—The thyroid body, or gland, as it is sometimes called, is a soft, and very vascular organ, situated upon the lateral aspect of the upper part of the trachea, as far upwards as the sides of the larynx. It consists of two lateral lobes, united by a thin narrow portion, which has a similar structure to that of the gland itself, extending across the front of the third or fourth rings of the trachea, and known as the isthmus. The middle lobe, which varies somewhat in position, is a thin process, extending upwards from the isthmus, or one of the lateral lobes, and often reaches as high as the hyoid bone, to which it is attached by loose fibrous tissue; indeed, this process itself is not unfrequently composed of fibrous tissue only, and sometimes contains a few fibres of the thyro-hyoid muscle.

The thyroid body itself, is made up of a vast number of small lobules, which are aggregated together in larger globular or oval masses, of which the entire substance of the gland is composed. These are all surrounded by, and connected together with, areolar tissue, and each subdivision itself consists of a number of small closed vesicles, between which the vessels ramify, also closely invested with areolar tissue, varying considerably in size, and containing fluid, or a thick gelatinous matter.

Each vesicle may, therefore, be described as consisting of a fibrous coat, composed of areolar tissue, internal to which there exists a delicate basement membrane, lined by cells of epithelium, which vary somewhat in character, but usually are seen as polygonal, or almost circular cells of a faintly granular appearance, and having a nucleus, which, however, is by no means invariably pre-

* On the constitutional and local effects of Disease of the Supra-renal Capsules," by Thomas Addison, M.D., Senior Physician to Guy's Hospital, 1855.

sent. In most instances, the vesicle can be seen to be lined with a single layer of this epithelium, and many free cells are usually found floating in the fluid contained in the cavity.

The fluid in the vesicles is coagulated by heat and nitric acid, and evidently contains a large quantity of *albumen.*

The stroma of the gland consists of fibres of both the white and yellow element, and it supports the blood-vessels, which are exceedingly numerous, and form a capillary plexus round each vesicle.

The lymphatics in the thyroid are numerous, but of their ultimate distribution nothing is known.

The following are analyses of the thyroid body, by Dr. Beale.*

	Human.	Ox.
Water	70·60	71·34
Solid matter	29·40	28·66
Fibrinous and albuminous matter, vessels, and fat	26·384	24·628
Extractive matter	1·70	—
Extractive matter, with gelatine	—	2·888
Alkaline salts	·50	·642
Earthy salts	·816	·502

Uses of the Thyroid.—Of the uses of the thyroid but little is known. The material found in the vesicles is of an albuminous nature. Mr. Simon has advanced the opinion that the thyroid acts as a diverticulum to the cerebral circulation, and that its nutrition bears a certain relation to that of the nervous matter of the brain. When the latter is quiescent, the thyroid is supposed to be active in removing from the blood, and storing up in its cells, certain constituents which are required by the brain only in its active state, and which are diverted to it when it resumes its activity. This view is based upon the important fact, that the arteries of the thyroid body arise in close proximity to those which supply the brain, the *superior thyroids* coming off from the external carotid, just immediately above the point of bifurcation of the common carotid, and the *inferior thyroid* arteries, from the subclavian, almost immediately opposite the origin of the vertebrals.

Thymus.—The thymus body or gland is an organ only distinctly recognisable during early life. It appears to reach its largest size between the first and third years; but much variation occurs in this point in different individuals. It lies partly in the thorax and partly in the neck, and is composed of two lobes, which

* Dr. Handfield Jones, article "Thyroid," Cyclopædia of Anatomy and Physiology.

vary considerably in size, sometimes the right and sometimes the left being the largest.

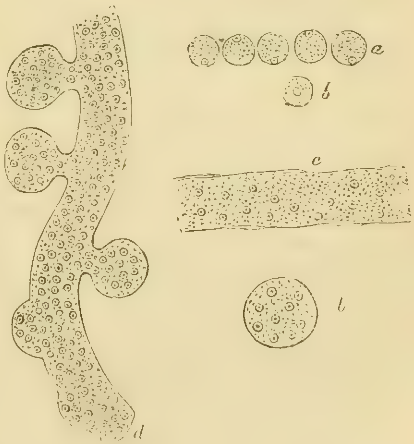
The organ rests upon the front of the aortic arch and large arteries rising from it, and also on the left vena innominata. It is covered by the sternum, and at birth reaches down to the fourth costal cartilage. It extends upwards into the neck, as high as the thyroid body, and lies upon the front and side of the trachea.

The researches of Sir Astley Cooper, and more recently those of Mr. Simon, show that this organ consists essentially of an elongated tube, from all sides of which extend numerous small follicles or sacculi, which pour their contents into the central cavity. Sir Astley Cooper unravelled the gland, and, by having previously injected the central cavity and follicles with alcohol, or coloured size, was enabled to make out their relations and arrangement; although, by these processes, it is probable that he distended the central cavity to a greater extent than natural, and was thus led to look upon it as much more extensive than it was subsequently proved to be by the conclusive observations of our friend Mr. Simon, which are published in his well-known essay.

The latter excellent observer, carefully watched the development of this gland, and thus was the first to make out accurately its anatomy.

It is probable that it first arises from a row of cells arranged in linear series, which coalesce, and thus become converted into a narrow tube. The wall of this tube then bulges at intervals, and vesicular cavities are gradually formed. These vesicular dilatations are much more abundant in some situations than in others; and the primary offset divides in a dichotomous or quaternary manner, until, from the number and irregular distribution of these vessels, the gland assumes its ultimate shape and character.. The closed cavity

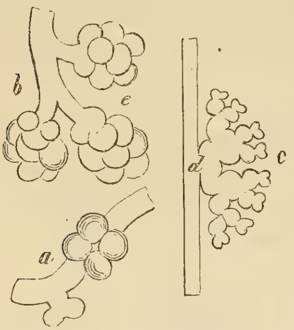
Fig. 250.



a. Primordial cells in a row. *b*. Isolated cell, unconnected with the row, and undergoing development in its original cell shape. *c*. Primary tube, formed by the fusion of the cells. *d*. Second stage of development of the thymus, showing bulgings of tube in different stages, which ultimately become themselves divided. After Simon.

of the gland contains granular matter, with numerous nuclei dispersed through it. In a thin section, the outline of the cavities can be readily seen; they vary from the 1-50th to the 1-18th of an inch in diameter, and contain numerous granular and nearly spherical nuclei, which are, for the most part, about 1-4000th of an inch in diameter, but vary considerably in size. Dr. Handfield Jones observes, that before any appearance of atrophy has taken place, these elements are alone found, and there is an entire absence of oil particles, and granular material. The nuclei seem to fill the ultimate vesicles completely.

Fig. 251.



a. Binary and quaternary division of simple follicles. *b.* Unusual appearance, in which the follicles must have increased considerably in length before undergoing division. From the fœtal lamb.
c. Mature structure of thymus, showing the arrangement of the vesicles belonging to one cone. *d.* Tube of gland. After Simon. Reduced.

Uses of the Thymus.—Mr. Simon regards the secretion of the thymus as allied to proteine, and of a nutritious nature.

In the human fœtus, the thymus cannot be detected before the ninth week, and its functional activity is greatest in the early period of life, before the muscular system is in a very active state; for when the muscles become more fully active, the thymus appears not to be required. It seems connected with the preparation of matter for the pulmonary organs in the "age of early growth." Arguing from these and many other facts, Mr. Simon looks upon the thymus as acting " as a sinking fund in the service of respiration." From the twentieth to the twenty-fifth year it diminishes rapidly in size, until no trace of it can be detected in the areolar tissue of the mediastinum. In hybernating animals, previous to the commencement of the winter sleep, the thymus becomes gorged with fat, which is slowly consumed during the period of hybernation. It has been remarked, that the use of the thymus at the different periods of active growth and hybernation is distinct. In the latter case, it doubtless supplies hydro-carbonaceous matter for respiration; but its office, during the former period, appears rather to be that of elaborating fibrine from albumen and other substances by the action of its numerous nuclei. As the absorbent and other glands connected with the vascular system become developed, there seems no longer any need of a special organ for this pur-

pose, and consequently the thymus soon disappears. Professor Paget and Dr. Handfield Jones express themselves in favour of this latter view. In the present state of our knowledge, perhaps no better hypothesis of the office of this gland can be suggested. The whole subject of the physiology of the vascular ductless glands (if glands they be) is involved in deep obscurity, and it is impossible to form a theory of their respective functions which is perfectly satisfactory. Not less obscure are their morbid conditions, upon which the improved anatomy of the last few years has thrown but little light.

The student is referred to the following works for a more detailed statement of the various views now held upon the anatomy and physiology of the vascular glands.

Spleen.—Kölliker's "Mikroscopische Anatomie," and the Article "Spleen," in the Cyclopædia of Anatomy and Physiology; Ecker's Art. "Milz," in Wagner's Handwörterbuch; Sanders "On the Structure of the Spleen," in the Annals of Anatomy and Physiology; Bennett "On Leucocythemia;" Mr. Gray's Astley Cooper's Prize Essay upon the "Structure and Use of the Spleen," 1854; Mr. Simon's Astley Cooper's Prize Essay on the "Thymus Gland," 1845; also his paper upon the "Thyroid," Phil. Trans., 1844; Dr. Handfield Jones' Articles "Thymus" and "Thyroid," in the Cyclopædia of Anatomy and Physiology.

CHAPTER XXXVI.

ON GENERATION.—FISSIPAROUS MULTIPLICATION.—GEMMIPAROUS MULTIPLICATION.—TRUE GENERATION.—METAMORPHOSIS.—METAGENESIS, OR ALTERNATION OF GENERATIONS.—SEXUAL ORGANS.—INVERTEBRATA.—INFUSORIA.—POLYPS.—ACALEPHÆ.—ECHINODERMATA.—ENTOZOA.—ANNELIDA.—MOLLUSCA.—CRUSTACEA.—INSECTA.—PISCES.—REPTILIA.—AVES.—MAMMALIA.

Amongst the lower classes of organised beings, both in the animal and vegetable kingdom, the multiplication of individuals, or the propagation of the species, is provided for by three different processes, while in the highest forms of animal life the process of generation is restricted to one of these types.

The simplest manner in which the multiplication of individuals takes place, consists in the division of the being into two, each of these again dividing into two others, and so on; this is multiplication by fission.

The second mode of increase consists in the formation of a bud at some part of the body of the parent: this bud is gradually developed, drops off, becomes independent of its parent, and ultimately assumes a perfect form, resembling in all particulars that from which it sprung.

The third mode differs materially from the two former, in the fact, that the new organism results from a series of changes occurring in an impregnated ovum, which is produced by the mutual action of the contents of two dissimilar cells, the products of distinct parental organs. The new body differs essentially from either of the two cells which produced it. This is *true generation.*

Fissiparous Multiplication.—In the lowest plants, such as the lichens and fungi, this mode of multiplication very commonly occurs. The cell, or cells, of which the plant consists, divide and sub-divide; and, in this manner, new organisms are produced. The same mode of reproduction is also seen to be very common amongst the Infusoria, and may be watched in the common vorticella.

Fig. 252.

Vorticella Microstoma multiplying by spontaneous longitudinal division, from Ehrenberg.

The joints of the common tape-worm multiply in this manner, and after a time, when perfectly developed, become free and separate from the trunk of the worm. Amongst the worms (Annelida) reproduction takes place partly in this manner. In the Naïs, three or four young worms, resulting from the division of the parent, may often be seen still connected with its body. As these become developed, they are disconnected from the parent and, in their turn, give rise to others by a similar process.

Fig. 253.

Naïs proboscidea, multiplying by spontaneous transverse division, shewing the body of the parent worm and three young ones in different stages of development. *a.* Point at which new segments are being formed, after Müller.

In the above instances, multiplication by division occurs as a natural process; but there are many instances in which the parts resulting from *artificial* division ultimately become developed into a perfect animal. Thus a planaria, or a polyp, may be divided into many segments; and each portion has the power of absorbing to itself nutriment, and of becoming developed into a perfect form. The slightest handling, again, causes some animals to break up in pieces, and each separate part becomes a new being.

Multiplication by Gemmation.—A bud consists of a mass of cells,

which possess the power of development, under favourable circumstances, into a form identical with that from which they were produced. In consequence of this property, the bud of a plant has been termed a *phyton*; and a tree must, therefore, be looked upon as an assemblage of these phytons. We must, however, bear in mind, that all buds have not this power, as, for instance, flower buds do not give rise to the formation of new buds of any sort, but produce seeds.

Amongst the lower animals, reproduction by buds is very common, and can be readily examined in the vorticellæ and polyps.

Fig. 254.

Figures of the fresh-water hydra and vorticella, shewing the multiplication of new individuals by the formation of buds.

In the hydra, the first change which is observed consists in the formation of a little elevation which soon becomes globular; next a cavity is formed in this globular mass, and becomes continuous with that of the parent. After a time the channel of communication closes, and the bud begins to assume the form of a polyp, which ultimately drops off; and in this way a new creature is formed. The echinococci multiply by the formation of buds upon the internal surface of the hydatid vesicle. At first they are attached by a sort of stem; but ultimately they become free, and move about in the fluid of the parent cyst by aid of their hooks and suckers.

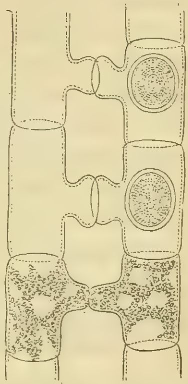
A bud differs from an ovum in the important particular, that it contains within itself the power of development, while the latter is incapable of becoming developed into the form of its parent until it has been subjected to the action of the contents of another cell. The only resemblance between a bud and an ovum is, that in both the organization is imperfect.

True Generation.—The processes of multiplication above referred to must be distinguished from the one which we are now about to consider. True *generation* consists in the union of the contents of two different cells, called respectively the "sperm cell" and "germ cell," and the production of a structure differing from both, from which the new being is ultimately evolved. The simplest form of this process is seen in the lower algæ in *conjugation*. At first, the opposite cells of two filaments are seen to be swollen on the

side turned towards each other; the swelling increases until a sort of process is formed from each: these at length meet; the walls become fused, the cavities continuous, and the contents of the two cells become mixed. From this admixture a new body, termed a *spore* or *sporangium*, results, by the development of which the new plant is formed.

In the higher plants and in animals, distinct organs are set apart for the formation of the sperm cells and germ cells. By the action of the contents of the sperm cell the ovum becomes impregnated; and under favourable circumstances, often quite independent of the parent, changes result which give rise to the formation of the embryo from which the adult animal is gradually developed.

Fig. 255.



Conferva bipunctata in the act of conjugation, after Meyen. The cells from contiguous filaments approach each other, and ultimately their cavities coalesce. The oval spores resulting from the action of the contents of one cell upon the other are seen in two of the cells.

Now, either the perfect form of the being may be attained by the gradual and progressive development of the embryo, or several distinct *phases of existence* may be passed through before the creature reaches its perfectly developed form. This latter condition is seen in many of the lower classes of animals, and is familiar to us in the class of insects; it is, in fact, what we understand by *metamorphosis*.

Metamorphosis.—In metamorphosis, it must be carefully borne in mind, that it is the self-same embryo which passes through certain transitional stages or phases, and ultimately becomes the perfectly developed animal; a condition essentially different from that which we shall next consider under the term *Metagenesis* or *alternation of generations*, in which successive generations of larval creatures are produced from larvæ without the occurrence of any fresh generative act. Here, instead of one individual passing through several transitional forms, an *imperfectly* developed creature produces a multitude of forms resembling either itself or the perfect individuals from which the ovum was formed which evolved it.

Metagenesis.—In some animals, the embryo, instead of being developed into a form resembling that of its parents, only attains a sort of larval condition, the offspring of which, however, return to the perfect type, instead of assuming the character of their larval parent. Now, between the fully-developed animals of one

generation and those of the next succeeding there may be several series of these imperfect or larval forms; each larva producing without any generative act, and, indeed, without itself possessing true generative organs, many similar larval forms, until at last these larvæ, instead of producing larvæ, give rise to perfect forms, which propagate only by the production of ova.

This curious phenomenon occurs amongst many classes of animals; and the subject of late years has engaged the attention of many naturalists. Steenstrup has described the process under the term *alternation of generations.* Owen terms it *metagenesis* and *parthenogenesis.* The facts have been explained differently by different observers; the two most important theories being the following: according to the first, the subsequent broods result by a process resembling budding, taking place within the bodies of their predecessors; while the second supposes that a portion of the original germ-mass is actually transmitted from the parent through the whole series of beings existing between two generative acts. The latter view has been most ably advocated by Professor Owen, in his lectures on *Parthenogenesis;* and the former is supported by Dr. Carpenter. In the Campanularia dichotoma, one of the tribe of polyps, at certain periods, buds are developed from the stem, which do not become converted into polyps, but, after having reached a certain stage of development, drop off, and in their mature state are seen as transparent disc-like bodies, having the power of swimming about in the water. These creatures have long been known as Medusæ, or jelly-fishes. It must be remarked, that no generative organs are to be found in the polyp; but these organs are found in the Medusæ, in which also ova are developed. The ova become polyps, which eventually put forth Medusa-buds as before.

In another polyp, the Strobila, at certain periods, multiplication by the formation of buds ceases, and the body of the polyp becomes constricted, and at the same time much elongated. The constrictions, which may be as many as forty in number, gradually become deeper, until at length the body of the polyp becomes divided into a number of flattened discs. The terminal disc drops off, and appears as a free swimming Medusa, in which generative organs are found and ova produced. The other discs fall off successively, and in like manner become Medusæ. These polyps, therefore, would with propriety be considered as belonging to the class Acalephæ, the Medusa representing the perfect condition of these animals.

The livers of various animals are infested with an entozoon termed a fluke. The development of the fluke of the common fresh-water snail (Limnæus stagnalis) presents us with a beautiful example of the curious phenomenon we are now considering. In the first stage of its existence it is seen as a creature (Cercaria) swimming about in the water, and is provided with a tail. After a time these cercariæ fix themselves to the skin of the snail by means of a circlet of hooks. The tail is cast off, and the body becomes covered with mucus, which hardens, until a transparent case is formed. This is the pupa state. Next the creature bores its way into the body of the snail, and reaches the liver; the hooks drop off, and it possesses all the characters of a fluke or distoma. The fluke develops ova; the ova become developed into worm-like creatures, which inhabit the snails. The worm-like body contains, as it were, a progeny, each member of which becomes the parent of another generation. The original larvæ are developed from a perfectly spherical germ, consisting of granules. So that the early stages of life of the fluke are passed in the body of a worm-like creature; the next in the water, free; next, attached to the body of a snail; and, lastly, in a perfectly-developed form in the liver. Thus this creature assumes three distinct forms at different periods of its existence, which, until these discoveries were made, had been described as three distinct creatures.

There are numerous other most striking instances among the entozoa of this extraordinary change of character in the course of development. It has long been known that the cystic entozoa (as Cysticercus, etc.) are not provided with generative organs; but it was reserved for Van Siebold to show that these entozoa were only the imperfectly developed forms of species occupying a higher position; and he has been able to prove that the *cysticercus fasciolaris*, which is found in the liver of the rat and mouse, becomes developed in the intestine of the cat into the *tænia crassicollis*, the common tape-worm of that animal. Kuchenmeister and Van Beneden have been able to demonstrate the occurrence of similar changes in many other entozoa.

Another beautiful example of *metagenesis* occurs among the members of a much higher class of animals—insects. The ovum of the perfect winged aphides, or plant lice, becomes developed into an imperfect wingless or larval creature, in which no sexual organs have been discovered. These viviparous but non-sexual larval forms are capable of producing non-sexual descendants, exactly resembling them, without the occurrence of any generative act,

and this process is repeated for nine or ten generations. The last autumnal brood, however, of these larvæ produce in the same viviparous manner perfect male and perfect female insects, with fully-developed sexual organs. The female deposits her ova in the axils of the leaves and other protected parts of the plant, where they remain till the following spring, when they are hatched, and the larvæ above-described issue forth :—the first larva producing eight, and each of these repeating the process, until, in the course of the summer, millions of larval forms are produced. This must conclude our very imperfect sketch of these interesting processes; and, for more detailed information, we must refer the reader to the works enumerated at the end of the present chapter.

Professor Owen considers that the larval forms result from the development of a portion of the original germ-substance of the yolk, which was not converted into a portion of the textures of the beings which resulted from the immediate development of the ovum; and hence he has applied the term *parthenogenesis,* or virgin generation, to this process of development. Dr. Carpenter, on the other hand, looks upon the process as akin to gemmation, or budding, rather than one of *actual generation.* Victor Carus shows that in this process of development the embryo is formed from a granular germ, whereas ordinarily it results from the process of cell-multiplication, as will be shown in the chapter on the development of the embryo. The same author contrasts the process of metamorphosis and metagenesis in the following words: "Larvæ, the subjects of metamorphosis, arrive at the state of perfection by throwing off provisional structures which belong to their larval condition; but nurses,* the subjects of metagenesis, are themselves entirely provisional structures."

In the present state of knowledge, it is difficult to group these extraordinary phenomena under one general head. Although we may contrast the processes of metamorphosis and metagenesis with each other, and draw definite distinctions between them, we must remember that there are instances in which both these processes occur; and although metamorphosis affects a single individual, and metagenesis a very numerous progeny, we do not feel ourselves in a position to define the exact relation which one bears to the other, and we think it better to avoid any attempt at generalisa-

* The term "nurse" was originally applied by Steenstrup to these larval forms, but we have purposely avoided its use, as it is for many reasons very objectionable and likely to convey a wrong idea of the nature of the viviparous larvæ.

tion until a greater number of facts relating to these wonderful processes should be discovered, rather than adopt a view which future research may show to be erroneous.

Sexual Organs.—The generative organs are of two kinds, the male and the female organs, the one secreting the "sperm cell," and the other the "germ cell." The generative apparatus consists of two parts: a formative organ, in which the elements are produced, and which is *essential;* and an efferent duct, by which the products of secretion are carried off.

The male and female organs may exist in one individual or in separate individuals. The first condition is termed *unisexual,* and the second *bisexual* generation.

In some unisexual or hermaphrodite animals, self-impregnation takes place, as is the case in the common tape-worm (Tænia solium); while, in other instances, concourse is necessary in order that the ova should be exposed to the action of the spermatic fluid; this is the case with many of the mollusca, as the common snail, etc. In these instances, each hermaphrodite animal impregnates its neighbour.

Besides the secretion of the formative organ, other secretions are frequently poured into the efferent duct. The duct undergoes great modifications in different parts of its course in various animals, according to the particular office it has to fulfil. We shall now consider some of the most important characters which the sexual organs exhibit in the different classes of animals.

INVERTEBRATA.

The *Infusoria* multiply by fission, and rarely by gemmation. No sexual organs have yet been discovered in them, and ova are not met with in this lowest class of the animal series.

Fission may occur in the longitudinal direction, as in the *Vorticella:* or transversely, as in *Stentor* and some others; or in both directions, as in *Bursaria, Paramœcium,* and others. The Vorticellæ are also propagated by the formation of buds. When division is about to take place, the cell within the body, known as the nucleus, is seen to divide into two; each half containing, therefore, a newly-formed nucleus.

The *Polyps* multiply by gemmation and by the formation of ova, very rarely by fission. In gemmation, the young polyp may be ultimately set free, as in the *Hydra;* or it may remain attached to the stem or common body, or polypidon, as in the majority of the members of this class. Some polyps are hermaphrodite, while in many the sexes are distinct. At the time when the common hydra is about to propagate by ova, the male and female organs are both developed as excrescences upon the outer surface of the body. Others, again, are sexless, and give rise to the development of medusa-buds, or split up into discs, as already described in p. 528.

Reproduction in the class *Acalephæ* takes place almost entirely by the formation of ova. It has, however, been shown by Professor Huxley, that some multiply by gemmation as well as by the production of ova (Diphyidæ). Some of the species are unisexual, and others bisexual. The genital organs are only developed at certain periods, and the male and female elements are brought into contact through the influence of the water in which they swim.

In the *Echinodermata*, fission has only been observed to occur in one class (Holothuria); and the generative function, which is developed in this class to a great extent, is carried on almost exclusively by the production of ova. The sexes are distinct, but the ova are impregnated without sexual intercourse. In some there is a proper efferent duct; but in others the elements pass into the respiratory cavity, and thus escape from the body.

Among the *Entozoa* great variety is met with in the arrangement and character of the generative organs. Almost all the animals of this class possess true generative organs, and multiply by means of ova, but in many of them fission occurs; as, for instance, in the tape-worm; but it is worthy of remark, that the entire animal is not produced in this process. The segments, however, which have been separated continue to live. As already mentioned, the Echinococcus multiplies by the formation of buds.

Some of the Entozoa are unisexual, and have the power of self-impregnation, and some are bisexual.

The *Annelida* reproduce by sexual apparatus, and in some instances, as already referred to, by transverse fission. In the latter case, the different organs, including the tentacles and eyes, are developed before the new animal is separated from the old one. This mode of multiplication, however, only continues for a certain time; at length it ceases; genital organs, which before could not be distinguished, are developed, and ova are formed. The Hirudines and Lumbrici are hermaphrodite, but copulation is necessary for impregnation to take place.

Amongst the lower *Mollusca*, the sexes are sometimes united in one individual, and sometimes distinct. There are no copulatory organs, so that the water forms the medium by which the spermatic particles are conveyed to the ova. Amongst the Tunicata, multiplication also takes place by gemmation.

Of the higher *Mollusca*, some are hermaphrodite, and in others the sexes are distinct. Many families are characterised by the possession of what has been termed an hermaphrodite gland, which is almost always imbedded in the substance of the liver. This gland consists of numerous radiating and branched cœca. Each cœcum consists of an external and internal sac folded within the first. Ova are produced by the external sac, and spermatic particles by the internal one. Excretory ducts pass off from these organs, and terminate in two tubes; the one corresponding to the Fallopian tube, the other to the vas deferens. Besides this apparatus, there is also another organ connected with the excretory duct; this is the albumen gland, which furnishes a secretion in which the ova become imbedded as they pass towards the external orifice. This curious arrangement may be well seen in the common snail.

Into the same cavity or cloaca in which the genital ducts terminate, is found the opening of another very remarkable organ—the dart sac—in which a hard and excessively sharp-pointed, and sometimes toothed, calcareous body

is formed, which is projected during copulation. The dart may be looked upon as an arrangement for producing sexual excitement, for each snail has been seen to prick the other just before coition.

Amongst the *Cephalopoda*, the highest of the Mollusca, the sexes are always distinct. Connected with the excretory duct of the ovary is an apparatus which furnishes a secretion by which the eggs are bound together, and a firm horny covering formed for their protection.

The testicle consists of an oblong organ, situated at the bottom of the cavity of the mantle. Connected with the excretory tube, is a sac in which some very complicated organs, containing the sperm, are developed, from which the contents are expelled by a very remarkable projectile apparatus. Coition appears to take place simply by one animal applying itself to the other. A true intromission of the penis seems hardly possible.

One of the most curious phenomena which has been discovered in connection with the generation of some of the members of this class must be briefly noticed here. On the male Argonaut is developed a curious elongated body, termed Hectocotylus, which communicates with the testicle of the Argonaut by a duct. Before this body had been proved to belong to the male Argonaut, and had only been seen upon the female, it was looked upon as a parasite, and Cuvier described it as one of the Trematoda. The Hectocotylus, which is to be regarded as one of the arms of the animal metamorphosed in a peculiar way, at length becomes filled with spermatic fluid, and drops off. It is now independent, and comes into contact with the female Argonaut, which it impregnates. In this point it resembles, "as also by its movements, by a kind of circulation, and by the long duration of its life after detachment, a true male animal" (H. Müller).

Among different families of the *Crustacea*, the arrangement of the generative organs varies much. In most, the sexes are distinct; but one class, Cirrhipoda, is hermaphrodite. Some Crustacea, again, are almost exclusively females; and these for many generations produce females, and at very long intervals only, males. Some females, again, lay two kinds of eggs, one of which becomes developed spontaneously, while the other requires to be fecundated by the spermatic fluid. The female of the Daphnia, towards the close of the year, produces two eggs, which must be looked upon in the light of gemmæ, or buds, as they contain no germinal vesicle. These are the so-called hybernating eggs, and are developed without the fecundating influence of the sperm.

Among the Crustacea, the genital organs are usually double, and symmetrical in both sexes. Connected with the efferent duct of the female organs are some glands, which secrete a viscid substance, by which the eggs are glued together in clusters to the posterior abdominal feet, as occurs, for the most part, among the Decapoda (lobster, etc.); but in those species in which these organs are deficient, there is formed a marsupium, or sort of pouch, connected with the lower surface of the thorax, into which the eggs are received and retained until the young escape. The greater number of the Cirrhipoda are hermaphrodite; but it has been shown by Goodsir that this is not a universal characteristic of this class.

Among the different families of the large class *Insecta*, the arrangement of the generative organs presents great variety. The sexes are always distinct, and impregnation is invariably effected by copulation; hence, the external

aperture of the efferent duct is found to be variously modified, according to the different circumstances in which the animal lives, and the modification of its general form. In some classes, the females are very few in number, and often whole colonies are developed from one female. This is the case amongst the bees, termites, and ants, in which the great majority of the individuals are found to be neuters or workers. In the pupa of these last, the generative organs may be distinguished, but they afterwards become atrophied. Now it appears probable, that the development of the female organs is dependent upon nourishment; for it has been found, that the larvæ which are to become fertile females, or queen bees, have been supplied with a much more stimulating kind of food than that upon which the workers have been fed.

The generative organs are double and symmetrical in insects, and several accessory organs are found connected with the efferent duct. Of these, the most remarkable is a receptacle connected with the vagina of the female, designed to receive the seminal fluid of the male. This vesicle is termed the *receptaculum seminis,* and in it the spermatic particles of the male may be kept in a living condition for a very long period of time. The ova are impregnated as they pass the orifice of the duct of the receptaculum seminis. Besides this last, there is another organ connected with the lower part of the female genital organs, designed to receive the penis of the male. This is known as the *bursa copulatrix,* which, however, is not universally present. Mucous glands pour their secretion into the vagina near its external orifice.

The arrangement of the *ovaries* differs considerably in various classes. The gland usually consists of cœcal tubes, which are four or five in number, and open into the summit of the efferent duct; while in some the tubes open separately in the sides of the duct. The number of secreting tubes is very variable in the different classes.

The *testicles* consist of two or more (and often there are very many) simple cœcal tubes, the arrangement of which varies much, and which open into the vas deferens of the corresponding side. The vasa deferentia are often very long and much convoluted; in some instances they are dilated below, so as to form a sort of vesicula seminalis.

The copulatory organs vary much in their disposition; usually they consist of hard, horny valvular appendages. In some species, suckers are developed upon the legs; and other arrangements are found for the purpose of retaining the female during the act.

The imperfect or larval form of many insects when they leave the egg, has already been alluded to under the heads of metamorphosis and metagenesis, or alternation of generations.

Vertebrata.

In the vertebrata, with the highest and most perfect development of the generative function, we shall find the progressive elevation characterized by greater complexity of structure, more protracted dependence of offspring on parent, and closer relations of the two sexes.

Fishes.—There are three types of structure in the generative organs of fishes. First, in the Cyclostomatous Group and in the Eel, the ovary consists of membranous folds depending from the spine, between the layers of which the ova are, at the spawning season, developed. When mature, they escape by the rupture of the membrane into the general peritoneal cavity, in which

they may be found in large numbers, and from which they escape by a small opening situated near the anus. The male organs are to the unaided eye so like the female, that it is only in the spawning season that they can be distinguished: the spermatozoa escape into the peritoneal cavity in the same manner as the ova. Secondly, in the Osseous Fishes the ovary, or *roe*, consists of a large membranous sac, enclosing the ovigerous folds, between the layers of which the ova are developed just as in those we have described, so that when the ova escape they are discharged, not into the general peritoneal cavity, but into this ovarian sac, and thence find their way out by a tubular prolongation of it, or excretory duct, which opens just behind the anus. The testicle is strictly analogous. In neither of these classes does copulation take place; the spawn is cast abroad into the water, and left to be fecundated by the sperm discharged over it by the male, to be devoured, or to perish in an unfecundated state, as chance may direct. One of the most remarkable points in the history of osseous fishes is their immense fecundity: it is calculated that a Cod discharges nine millions of ova in a single spawning season. The reason of this unparalleled fertility appears to be, that there may be the greater chance of *some* escaping and surviving the many perils to which they are exposed. Thirdly, in the Cartilaginous Fishes, as the Sharks and Rays, we have a much higher type of the generative function. Copulation takes place; the male is furnished with an intromittent organ, and with certain accessory parts, called "claspers," for seizing and embracing the female during the act of impregnation. In the female, the ovaries are racemose, from the increased size and diminished number of the eggs, which, instead of escaping into the peritoneal cavity, are seized by the patulous orifices of two long oviducts, whereby they are conveyed out of the body, and by which they are furnished with that peculiar horny shell, which serves at once to protect and to attach them to some fixed point.

Reptilia.—The *Amphibia* exhibit, in the function of generation, an interesting link between the piscine and the true reptilian structure; there is no intromittent organ, and yet copulation takes place, and the ova are fecundated neither after extrusion, as in the osseous fish, nor before extrusion, as in true reptiles, but during the very act of discharge, *in exitû.* At the commencement of the spawning season, a remarkable papillary structure is developed on the thumbs of the male frogs, highly sensitive, and giving rise, when stimulated, to a forcible reflex action, by which the upper extremities are approximated, and tightly embrace anything placed between them (vol. i. p. 335). By means of this, the male frog firmly embraces the female, and continues to do so through the whole time of the expulsion of ova, without any expenditure of voluntary action, and impregnates the ova as they pass from the female beneath him. The vas deferens passes through the structure of the kidney, and opens at once into the ureter, the two being thence continued as one duct—a sort of prolonged genito-urinary cloaca. In the *Triton*, we go a step further, and find the ureter and vas deferens distinct to their termination, and impregnation taking place internally, although there is no rudiment of a penis. The *Ophidians* present a further advance, and show the first trace of a penis: it consists of two erectile corpora cavernosa, which, however, are quite separate, and constitute rather an organ of prehension than of intromission. In the *Saurians* and *Chelonians* another step is gained, and the two corpora cavernosa are united in the middle line; there is still, however, no

corpus spongiosum, and no prolongation of the urethra, but the seminal secretion passes into the female along the groove formed by the union of the two cavernous bodies.

Aves.—The generative organs of birds exhibit a close analogy to those of the higher reptiles, the penis is even less developed, except in the struthious birds (ostrich) and the swimmers. The ovary is racemose and single, the right with its oviduct being permanently atrophied; a singular violation of symmetry which is confined to birds. In this class of vertebrata, incubation, that singular substitute for utero-gestation, attains its highest perfection: it appears to arise from the concurrence of these three exigencies—the necessary size and early maturity of the young, the necessity of warmth to their development, and the incompatibility of utero-gestation with flight.

Mammalia.—It is from the possession of a remarkable accessory organ of generation, that this important class of the highest organised beings takes its name. After all organic connection has ceased, the young are still dependent on the parent for nourishment, and are supported by the secretion from a special gland with which the female is furnished for the purpose—the mammary gland. The mammalia are divided into the *monotremata*, the *marsupialia*, and the *placental mammalia.* The monotremata are as yet imperfectly known, but they present a curious connecting link between the oviparous and mammalian type; they derive their name from possessing but one aperture, that of the cloaca, common to the generative, urinary, and digestive canals, and in this respect resemble birds; they are represented by the ornithorynchus and echidna of Australia. In the male, the penis is perforated by a urethral canal, through which the semen, but not the urine, passes: in the female, the ovaries are racemose, the ova large, and containing all the elements of an egg, and there are two uteri, opening by distinct apertures into the cloaca. The *marsupialia* (called so from the possession of a marsupium, or pouch, in which the young is lodged and suckled after its discharge from the uterus), are *ovo-viviparous*, that is, the young are brought forth alive, but they never have any placental connection with the parent. Not only are there two uteri, but two vaginæ, which terminate by two separate orifices in a sort of genito-urinary cloaca.* About thirty-nine days after conception, the young is expelled into the marsupium, where it becomes attached to one of the nipples by its mouth, and continues thus to draw nourishment from the mother for a period of eight months: this peculiar method of fœtal nourishment necessitates a very advanced and disproportionate development of the organs of assimilation, which is the most remarkable characteristic of the embryo marsupial. The *placental mammalia*, in the general structure of their generative organs, resemble man. The testicle consists of seminiferous tubules arranged in bundles, and enclosed in a fibrous capsule. The penis is composed of two corpora cavernosa arising from the ischia, a corpus spongiosum

* In the male, the testicles are contained in a scrotum placed above, and not below, the penis, in a situation analogous to the marsupium in the female, and supported, like it, by two marsupial bones; the vasa deferentia open into the urethra, which, invested by its corpus spongiosum, passes through the centre of the penis, and which now, for the first time, we find forming a complete canal, leading from the bladder to the extremity of the intromittent organ.

urethræ, and glans; and there are certain accessory glandular structures, vesiculæ seminales, prostate, and Cowper's glands, opening into the urethra in its course. Into the different numbers, modification, and structure of these organs it is not worth while to enter. In the rabbit, the ovary exhibits some trace of the racemose structure, and, by the different modifications of the uterus, dependent on the proportionate size of its body and cornua, we are conducted from the marsupialia, in which the two uteri are entirely distinct, to the human female, in which the single uterus exists in its greatest degree of concentration.

In writing the present chapter, the authors have received much assistance, from the following works:—Müller's "Elements of Physiology," by Baly; Professor Owen's Lectures "On Comparative Anatomy," and his treatise "On Parthenogenesis"; Dr. Carpenter's "Principles of General and Comparative Physiology"; Victor Carus' "System der Thierischen Morphologie"; Art. Ovum, in the "Cyclopædia of Anatomy and Physiology," by Dr. Allen Thompson; "On the Alternation of Generations," by Professor Steenstrup, translated by the Ray Society.

CHAPTER XXXVII.

MALE ORGANS OF GENERATION.—TESTICLES.—VASA DEFERENTIA.—VESICULÆ SEMINALES.—PROSTATE GLAND.—COWPER'S GLANDS.—PENIS.—URETHRA.—GLANDS OF LITTRE.—GLANDULÆ TYSONI.—VESICULA PROSTATICA.—SEMINAL TUBULES.—SPERMATOZOA.—DEVELOPMENT OF SPERMATOZOA.—MOVEMENTS OF SPERMATOZOA.

Male Organs of Generation.—The essential organ of generation, or the secreting portion of the sexual apparatus, in the male, is the testicle. The efferent duct is the vas deferens, which opens into the membranous portion of the urethra, and connected with it are the vesiculæ seminales and Cowper's glands. The urethra is continued forwards along the lower part of the penis, or *intromittent* organ.

Testicles.—Each testicle is rather less than two inches in length, and is nearly one inch broad.—Its weight is about six drachms. The testicle is covered by a firm, fibrous, inelastic tunic, or proper covering, the *tunica albuginea* or *tunica propria,* consisting almost entirely of white fibrous tissue, in the substance of which vessels ramify. It is with difficulty divided into two layers, the inner of which is the most vascular. Adhering closely to the tunica albuginea, is the visceral layer of the serous membrane, or *tunica vaginalis,* the sac of which was originally formed by the descent of the testicle from the abdomen, when it carries before it a process of peritoneum. In early life, the cavities of the tunica vaginalis and peritoneum are continuous with each other; and, occasionally, the opening remains unclosed in the adult. The parietal layer of the tunica vaginalis is loose, and united by lax areolar tissue to the other structures which form the scrotum. This layer of the serous membrane admits of considerable distension; and, in disease, a very large quantity of serous fluid will sometimes accumulate in the sac, and distend it to a great extent (*hydrocele*).

Structure of the Gland.—The secreting portion of the organ consists of a vast number of minute and highly tortuous tubes, which

are arranged in conical lobes, or parcels, each consisting of two or more tubes, which are covered with a layer of condensed areolar tissue, continuous with the *corpus Highmori*. These divisions are, however, not complete; for the tubes of one parcel communicate with those of the adjoining ones. The highly convoluted seminal tubes commence in blind extremities or in loops; and, after dividing frequently, and forming anastomoses, they become less tortuous as

Fig. 256.

a. Origin in blind extremities and branching of seminal tubules—human subject. *b*. One of the blind extremities more highly magnified.

they approach the mediastinum testis, where two or more unite to form a short straight duct, the *vas rectum*; these vasa recta again unite, so as to form a sort of net-work, the *rete testis*, which occupies the *mediastinum testis* or corpus Highmori. From the rete testis pass the *vasa efferentia*, which are usually about twelve or sixteen in number, and are much convoluted; and, by being packed together, form part of the epididymis. They open into a single and highly tortuous duct, the *vas deferens*, which is usually about sixteen inches in length, and forms a very hard, round efferent duct, readily distinguished, by the feel, from the other structures which compose the spermatic cord. The vas deferens is lined with a single layer of tesselated epithelium, and there is a layer of very lax areolar tissue beneath the mucous membrane, which would permit of great

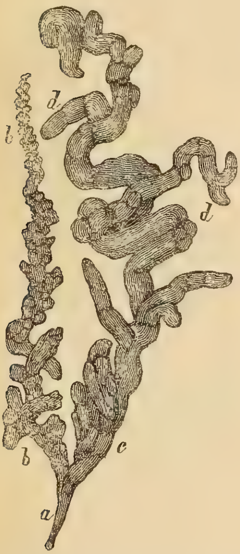
Fig. 257.

Transverse section of the vas deferens—a segment only is represented in the drawing—*a*. Lining membrane of the tube connected by a thick layer of lax submucous areolar tissue (*b*) to a thin longitudinal layer of unstriped muscle (*c*.) *d*. Layer of circular or transverse fibres. *e*. External thick layer of longitudinal fibres, surrounded by an outer covering of areolar tissue. *f*. From a drawing by Dr. Beale.

increase in the diameter of the canal when it was distended with secretion, *b.* fig. 257. It passes behind the bladder, and terminates in one of the *ejaculatory canals*, a very short canal, which is formed by the union of the vas deferens with the corresponding *vesicula seminalis,* which is situated a little external to it, upon the posterior surface of the bladder.

Vesiculæ Seminales.—The vesiculæ seminales are two sacculated receptacles, about two inches in length and about three-quarters of an inch in breadth, situated upon the posterior aspect of the bladder, lying between it and the rectum. They converge towards the point at which they open, and almost meet. The narrow terminal portion (duct) lies for a short distance, previous to its opening in the urethra, surrounded by the prostate. Each vesicula may be unravelled, so as to form a cæcal tube, with several diverticula projecting from it. It is very much convoluted, and the convolutions are connected together with areolar tissue, to which arrangement the sacculated appearance is due.

Fig. 258.



Vesicula seminalis, after E. H. Weber. *a.* Ejaculatory duct. *b.* Vas deferens. *c.* Vesicula seminalis. *d.* Terminal diverticula.

The structure of the vesiculæ seminales is very similar to that of the vasa deferentia, but their walls are much thinner. There is an outer coat, composed of areolar tissue, in which numerous muscular fibre cells are found. They are lined with a thin layer of tesselated epithelium.

The vesiculæ are usually found to contain a viscid, mucus-like substance, which may be regarded as their secretion; and which, no doubt, is of a nature favorable to maintain the vital activity of the spermatozoa, and serves also to dilute the semen. These organs were formerly looked upon as the receptacles for the semen; but a comparison of their arrangement, and an examination of their contents, in the lower vertebrata, by no means confirms this view, as our friend, Mr. Pittard, has remarked. In the elephant, the vesiculæ seminales open into the vasa deferentia, as in man; but seminal reservoirs are also found in this animal. In man, however, spermatozoa are very generally found in them; and it is probable that they serve partly as receptacles for the semen,

but at the same time, there can be no doubt that they furnish a proper secretion of their own for its dilution, and for the preservation of its integrity.

Prostate Gland.—The prostate may be described as consisting essentially of two distinct structures; first, of a glandular portion, composed of conical or roundish vesicles lined with cylindrical epithelium and containing brown granules; and, secondly, of several layers of fibrous tissue, with which many fibres of unstriped muscle are everywhere incorporated; indeed, the proportion of the muscular and fibrous elements to the glandular structure, is so great, that Kölliker calculates that the latter does not constitute more than one-third part of the whole mass of the gland. The muscular fibres covering the prostate, were originally described by Mr. Hancock.

The secreting follicles open into ducts, which are lined with cylindrical epithelium, presenting similar characters to that found in the prostatic portion of the urethra.

The ducts, which are very numerous, open into the urethra, upon each side of the *caput gallinaginis.*

Little is known with reference to the nature of the secretion of the prostate, or of the function which it performs. The secretion is stated to be very similar in character to that of the vesiculæ seminales.

Small concretions, or prostatic calculi, are very frequently met with in the follicles of the gland, or are voided during life. They usually consist of phosphate of lime, with animal matter, and a trace of carbonate of lime; and are often remarkable for their perfectly spherical form and smooth glistening surface. They commence by the deposition of calcareous matter in the walls of large oval cells, which are, probably, altered epithelial cells of the gland itself. Dr. Handfield Jones has carefully investigated the formation of prostatic concretions.*

Cowper's Glands.—These small glands are two in number, and are situated anterior to the prostate, between the layers of the triangular ligament. Their somewhat long excretory ducts open into the bulbous portion of the urethra. They are composed of vesicles, lined with tesselated epithelium, which pour their secretion into ducts lined with columnar epithelial cells. As in the case of the prostate, the secreting portion of these little glands is imbedded in a fibrous stroma, which contains very numerous unstriped muscular

* Medical Gazette, Aug. 20th, 1847.

fibre-cells. The secretion of these glands appears to be analogous to ordinary mucus.

Penis.—The penis of man is a highly vascular organ, traversed on its inferior surface by the urethra; it is composed principally of erectile tissue, which is capable of being distended with blood. This erectile tissue is arranged in three distinct divisions termed the *corpora cavernosa* and *corpus spongiosum.* The corpora cavernosa penis are two in number, and are separated from each other, posteriorly, by a septum, composed of fibrous tissue; while anteriorly, they are connected together, and might be considered as one organ. In the middle line above, is situated the dorsal vein, and other vessels and nerves; while the corpus spongiosum urethræ is received into a groove beneath. In the posterior part of the organ, the corpora cavernosa are separated from each other by a considerable interval, and each is inserted into the rami of the ischium and pubis; these two diverging extremities of the corpora spongiosa are termed the *crura* of the penis.

The corpora cavernosa are invested with a layer of firm fibrous tissue, which contains numerous fibres of the yellow elastic element.

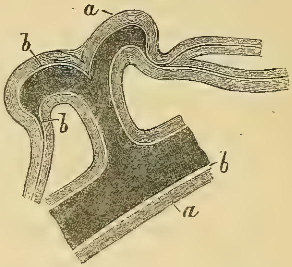
The *corpus spongiosum urethræ* surrounds the urethra, and commences behind, in a dilated portion situated between the crura penis; and it terminates anteriorly in the expanded *glans penis*, the rounded margin of which is termed *corona glandis*, and the constricted part beneath, the *cervix* or neck.

These bodies consist of a vast number of small venous sinuses, which communicate with each other upon all sides, and contain venous blood. The walls of the sinuses or *trabeculæ* are lined with a layer of tesselated epithelium, external to which is found the proper fibrous tissue, or *trabecular tissue.* This is composed of white and yellow fibrous tissue, and fibres of organic muscle. The arteries and nerves for the supply of the organ are supported and surrounded by this texture.

The *arteries of the penis* are branches of the pudic; and in their arrangement, present certain peculiarities, which are well worthy of notice. The smaller divisions, after pursuing a tortuous course in the trabecular tissue, at length open into the venous sinuses, without entering into the formation of any capillary plexus. In the posterior part of the penis, J. Müller discovered several minute arteries, which were much convoluted, and assumed the twisted appearance of tendrils; whence they were termed the *helicine arteries.* Kölliker has shown that these arteries terminate in minute vessels, and not in blind extremities, as was originally

supposed; the minute terminal vessels ultimately open into the venous spaces. The arrangement of the arteries in the corpus spongiosum urethræ, is similar to that just described.

Fig. 259.



A small artery of the corpora cavernosa, giving off a lateral branch, from which proceed helicine arteries, terminating in very small vessels, which are continued in the trabecular tissue, (*a*.) *b*. Wall of the arteries. After Kölliker.

Urethra.—The male urethra is the canal which extends from the neck of the bladder to the end of the penis. It is about eight inches and a half in length, but varies slightly in different cases. The tube itself is lined with mucous membrane, and its diameter is not by any means the same in its whole extent. Its direction is that of a double curve, like the letter *f*. The walls of the urethra are strong, and composed principally of fibrous tissue, with a layer of unstriped muscular fibre, the arrangement of which has been well described by Mr. Hancock.

The urethra is divided, by descriptive anatomists, into three portions; the *prostatic*, being about twelve lines long; the *membranous*, about three-quarters of an inch in length in its upper part, but only half an inch in its lower portion; and the remainder, by far the most extensive portion of the canal, called the *spongy portion*, which reaches to the orifice.

The *prostatic portion* of the urethra is its widest part, and lies imbedded in the upper part of the prostate, above its middle lobe.

At the neck of the bladder, the mucous membrane forms a fold, called the *uvula vesicæ*. Anterior to this is a narrow ridge, rising from the floor of the tube, about nine lines in length, and about one and a half lines in height in its highest part, called the *verumontanum, caput gallinaginis*, or *crest of the urethra.** On each side of this, the mucous membrane forms a depression, the prostatic sinus, into which the ducts of the prostate gland open.

At the highest part of the *verumontanum* is a little sinus, the *vesicula prostatica*. It is here that the ejaculatory ducts open.

The *membranous portion* is that narrowest part of the urethra which lies beneath the pubis and passes through the layers of the triangular ligament. It is surrounded with muscular fibres, and the *compressor urethræ* muscle is situated upon this part of the tube;

* Vide article "Vesicula Prostatica," in the Cyclopædia of Anatomy and Physiology, by Prof. Rud. Leuckart.

beneath it are Cowper's glands. This part of the urethra commences at the anterior extremity of the prostate, and terminates in the bulbous portion. Its upper surface is rather longer than the lower one, and it curves upwards.

In the evacuation of the bladder, it is most likely that the compressor urethræ muscle, which contains striped fibre, and guards the membranous portion of the urethra, becomes relaxed; then follows the relaxation of the sphincter vesicæ, and the contraction of the fibres of the bladder (detrusor urinæ), which causes the urine to escape from the urethra with considerable force.

The *spongy portion* of the urethra is about six inches in length, and is so called, because it is surrounded by the corpus spongiosum urethræ. That part of the canal in the bulb is somewhat dilated, but the diameter of the greater part of this portion of the canal is uniform. Cowper's glands open near the anterior extremity of the *bulbous portion.* When it reaches the *glans*, however, it undergoes another dilatation, the *fossa navicularis.* At its orifice, the urethra is contracted.

Mucous Membrane.—The short papillæ covering the *glans* become much elongated at the orifice of the urethra, and highly vascular papillæ are found in the anterior half of the fossa navicularis (fossa Morgagnii). They then cease abruptly, but re-commence in the posterior part of the glans, and are continued as far as the bulbous portion.

About one-third of an inch from the meatus, on the dorsal aspect of the fossa navicularis, is situated the *lacuna magna.* In other parts of the mucous membrane of the urethra, except in the prostatic portion, are numerous small lacunæ.

Glands of Littre.—The majority of these are simple involutions of the mucous membrane, or lacunæ; but some may be described as small branched glands or follicles, which are numerous in the cavernous portion of the urethra. These become more simple in the prostatic portion, and take the form of simple follicles.

The epithelium lining the urethra and the small glands just referred to, is for the most part of the columnar form.

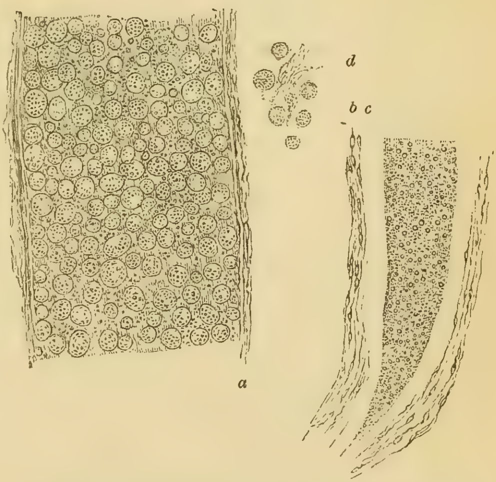
Glandulæ Tysonianæ.—These little glands are situated in the fold of skin round the glans penis. They are modified sebaceous glands, and the follicles of which they are composed, contain epithelium and fatty matter, resembling that which is met with in the ordinary sebaceous follicles of the skin. In this locality these glands open upon the soft skin of the prepuce, and are not associated with

hair follicles, as is usual in other situations in which they are found. The peculiar secretion known as the *smegma preputii,* is not due to these glands alone; but is rather to be regarded as an accumulation of the moist epithelium of the glans, which is, of course, mixed with the odoriferous sebaceous material. In the beaver, the epithelial secretion is so abundant, as to accumulate in large preputial pouches, the true nature of which was demonstrated by E. H. Weber. The secretion constitutes the substance known as castor.

Vesicula Prostatica.—Between the openings of the *ejaculatory ducts* in the middle line of the urethra, and in the substance of the *caput gallinaginis*, is a small cavity, lined with columnar epithelium, the *prostatic vesicle,* or *uterus masculinus,* as it has been termed by Weber, from its supposed homology with the female organ. It has since been described under the name of Weberian organ, from its discoverer.

Seminal Tubules.—The highly tortuous seminal tubes, of which the true secreting portion of the testicle is composed, consist of a fibrous coat, internal to which we find a basement membrane surmounted by epithelium. Now the characters of this epithelium, and the nature of the contents of the tube, will be found to exhibit different appearances, according to the age of the individual; and in the lower animals, according to the period of the year. Spermatozoa, which are the fertilizing agents, are not found before puberty in man, and among animals are only developed at certain periods. These bodies appear to be formed by certain alterations taking place in the character of the epithelium lining the tubes, for this latter is most distinct when spermatozoa are not being formed; but when the function of the gland is very actively

Fig. 260.



Portion of seminal tubules of man, with enclosed cells. Magnified 220 diameters. *a.* Wall of the tube. *b.* Nuclei of fibrous coat. *c.* Basement membrane.—The latter figure represents the action of acetic acid. *d.* Cells removed from the tubule.

performed, the tubes are seen to be entirely occupied by cells, in which the spermatozoa are ultimately developed.

When semen is about to be formed, the following changes may be observed to take place in the epithelium.

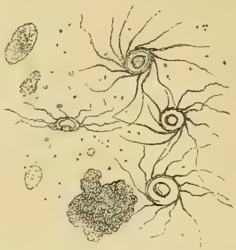
The cells become detached from the basement membrane, increase in size, and assume a more spherical form, the contents at this time being entirely granular; at length, however, several clearer points or nuclei are seen in the interior of the cell, which is now passing down the tubule towards the vas deferens, while it is succeeded behind by the formation of new cells. The nuclei in the interior enlarge, and are often seen to contain nucleoli. The parent cell, having much increased in size from the development of its nuclei into cells, appears to undergo no further change; but in each of the contained cells, which vary much in number, one spermatozoon is developed on the inner wall, in the form of a spiral filament, as was first described by Kölliker. The spermatozoon escapes into the interior of the mother cell by the rupture of its development cell. Others are in like manner set free; and they arrange themselves in a parcel, which may ultimately consist of a vast number of separate spermatozoa, with all the heads arranged in one direction and the tails in the opposite one.

The cause of this arrangement is probably somewhat similar to that which determines the blood disks to run together, and assume the form of a small pile of coins. There appears to be a sort of attraction existing between the different spermatic filaments for each other. The contained spermatozoa are at last set free by the rupture of the parent cell, and then separate. These changes are usually not completed until the cells arrive at the epididymis; so that in the seminal tubules cells alone are found, while in the vas deferens we only meet with perfectly developed spermatozoa.

Spermatozoa.—The spermatic filament or spermatozoon of man, is a perfectly clear hyaloid filamentous body, in which a dilated portion, termed the *body* or *head*, may be observed, from which is prolonged a long *tail* or *filament*, which gradually tapers to an extremity which is hardly visible from its extreme tenuity. The head or larger extremity is flattened from side to side and of a conical form, the pointed extremity being anterior. The length of the spermatozoon is about $\frac{1}{800}$th of an inch, and the width of the body in one direction about the $\frac{1}{5000}$th, and not more than the $\frac{1}{10000}$th of an inch in the opposite. The tail varies somewhat in length in different specimens.

The characters of the spermatozoa vary much in different animals; thus in the rat and mouse the head or body is unsymmetrical and curved. In the squirrel, the anterior extremity of the head is rounded, and wider than any other portion. In birds, the head is usually attenuated. In reptiles and fishes, the characters of the spermatozoa vary much in different examples. Among the invertebrata, those of the crustacea are very remarkable in form. For a detailed account of the characters of the spermatozoa in different classes of animals, we must refer the reader to the excellent article, Semen, in the Cyclopædia of Anatomy and Physiology, by Wagner and Leuckart.

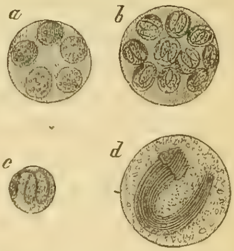
Fig. 261.



Spermatozoa of the river crawfish (astacus fluviatilis).

Development of the Spermatozoa.—The development of the spermatozoa has been carefully investigated by Wagner, Siebold, and Kölliker. The different stages are traced more readily in many of the lower animals than in man. In the rabbit, Kölliker has been able to observe the single spermatic filament within the cell attached to the wall and making two or three turns in a spiral form. It may now be looked upon as almost certain, that each spermatozoon is developed, not from any change of the cell, but from the contents within the cell itself. These cells are themselves developed in the interior of a larger or *mother* cell, into the interior of which the spermatozoa escape by the rupture of their developing cells, and are at last set free by the destruction of the wall of the parent cell itself. Professor Kölliker, in his latest investigations, has arrived at the conclusion that the spermatozoa are not developed *in* the nuclei of the cells, but *from* them. The nucleus becomes of an oval form, and one extremity is elongated to form the filamentary tail, while its principal part constitutes the body of the filament. In this case, they arrange themselves parallel to each other, the heads being in one direction and the tails in the opposite.

Fig. 262.



Development of the spermatic filaments of the rabbit. *a.* Parent cell, with five nuclei. *b.* Each nucleus of the parent cell containing a spermatic filament. *c.* Nucleus with spermatic filament. *d.* A parent cell with a number of spermatic filaments set free from the nuclei or cells of development.

Movements of the Spermatic Filaments.—When the spermatozoa have escaped, their active movements commence; and by the continual vibrations of the filamentous tail, they are propelled forwards, according to Henle, at the rate of one inch in seven minutes and a

half. The tail alone possesses the power of movement, and the force of the motion is sufficient to move objects many times the weight of the spermatozoon.

The movements are stopped by all those solutions which act chemically upon the spermatic particle. In water, the activity of the movements is at first increased, but it soon stops altogether, probably in consequence of endosmosis. Urine very soon puts a stop to the movements. The electric spark instantly stops the motions; but, according to Prevost, galvanism exerts no action upon them.

After spermatozoa have become quite motionless, and appear to be dead, movements may be excited by the addition of concentrated solutions of different substances, such as sugar, albumen, urea, and various salts. Caustic alkalies, in various degrees of concentration from $\frac{1}{30}$ to $\frac{6}{10}$, are special excitants of the movements. Moreover, Kölliker states, that semen dried in indifferent substances and in saline solutions, in certain cases may have its motion restored by dilution with the same fluid or with water. The motions cease in a high or low temperature.

In the interior of the female organs of generation, the movements continue for a longer period than in any other situation. In the receptacula seminis of insects, spermatozoa have been known to retain their power of movement for many months after they had been discharged by the male, and in the higher mammalia, the movement continues in the mucus lining the generative organs of the female, for many days after copulation.

It must be borne in mind, that the semen does not consist only of the secretion of the testicle, but that it also contains the secretions of the prostate, vesiculæ seminales, and Cowper's glands. What purposes these different secretions serve, it is difficult to say; but it is probable that they merely effect the dilution of the fluid in which the spermatozoa move, and thus render it a more favorable medium for their diffusion.

The movements of the spermatozoa have been regarded by some as due simply to the existence of endosmotic currents, while other authorities have attributed them rather to the inherent contractile property of the tissue of which they are composed.

The action of certain saline solutions upon these movements, does not seem, to us, to place this question in a much clearer point of view; since the mere physical alteration occurring in their contents would alone be sufficient to excite the contraction of the tissue of the spermatozoon.

That the spermatozoon is really the essential part of the semen, and is that in which all the mysterious fecundating power resides, may be now looked upon as proved beyond a doubt. The later beautiful observations upon the ova of the frog, of our lamented friend Mr. Newport, have shown that impregnation does not take place unless the spermatozoon actually passes through the vitelline membrane and comes into immediate contact with the yolk substance.

The chemical analysis of the semen has not led to any very important results The investigations of Frerichs are some of the latest that have been undertaken upon this subject. The most important fact which he has established is, that the spermatozoa consist of binoxide of protein, the substance of which epithelial cells are chiefly composed. The other constituents of semen are phosphate of lime, fatty matter, a certain quantity of extractive matter with alkaline sulphates and phosphates, and a small quantity of phosphorus in an unoxidized state. The imperfectly developed semen contains albumen, but this substance cannot be detected in the fully formed secretion.

From the various phenomena which we have been considering, and from many other facts which might have been brought forward, we are led to conclude that the spermatozoon is to be regarded in the light of an epithelial cell, or, rather, its nucleus, modified in structure and endowed with peculiar properties. Its mode of development, the continuous and obviously involuntary nature of the movements, and lastly, its chemical characters, all tend to this conclusion, while they place the originally received notion of the animal nature of the spermatozoon without the bounds of speculation.

Upon the nature of the force which is communicated by the spermatozoon to the ovum, we know nothing. Whether it is to be looked upon as a catalytic action, or whether the changes induced are of a chemical nature, are questions to which we can give no answer. Certain it is, that the integrity of the spermatozoon is necessary for fecundation. The spermatozoa of hybrids have been found, upon examination, to exhibit structural imperfections, and it has long been known that these animals are incapable of producing offspring.

That all the wonderful changes taking place in the ovum, which lead to the formation of the embryo and the development of the new being, result from the agency of the spermatozoon, is certain;

but *how* these are brought about, seems beyond the pale of human knowledge.

Upon the subjects treated of in the present chapter, the student may refer to Sir Astley Cooper's "Observations on the Structure and Diseases of the Testis"; Lauth's "Mémoire sur la Testicule Humaine"; Professor Kölliker's Microscopic Anatomy, and articles in the "Microscopical Journal"; Hancock, "On the Physiology of the Male Urethra"; Article "Semen," in the "Cyclopædia of Anatomy and Physiology."

CHAPTER XXXVIII.

FEMALE ORGANS OF GENERATION.—OVARIES.—GRAAFIAN FOLLICLES.—GERMINAL VESICLE.—PAROVARIUM.—FALLOPIAN TUBE.—UTERUS.—VAGINA, AND ACCESSORY ORGANS OF GENERATION IN THE FEMALE.—FEMALE URETHRA.

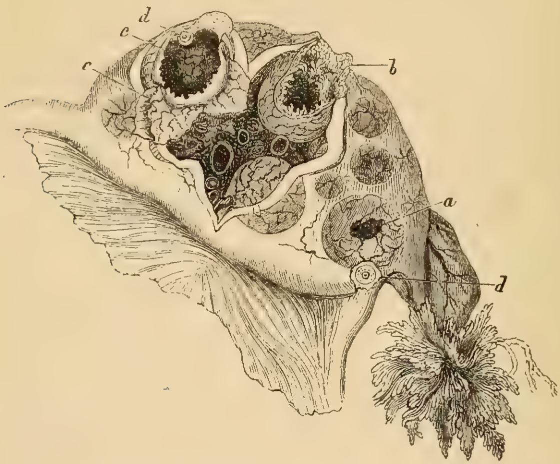
Female Organs of Generation.—The formative organ in the female is the *ovary*, in which the *ova* are developed and prepared for fecundation. From the ovary, the ova pass into the *Fallopian tube* or efferent duct, which opens into the *uterus*, the cavity designed for the reception of the ovum after it has been impregnated, in which the formation of the embryo takes place, and its development into the form of the future being occurs. From the uterus passes the *vagina* or tube which receives the penis of the male in copulation. With the vagina are connected certain glands and accessory organs.

Ovaries.—The ovaries are two in number, of an oval form, and flattened antero-posteriorly; they lie in the cavity of the pelvis, and are enclosed in a fold of the broad ligament of the uterus, with which organ they are connected by a narrow cord or *round ligament*. Each ovary is invested with a firm capsule of condensed fibrous tissue, which is covered with peritoneum, and is usually attached to the corresponding Fallopian tube by one of the fimbriæ of the latter. The ovary is composed of a firm, fibrous, and highly vascular stroma; in which are imbedded, at various intervals, a number of small cavities or vesicles, originally discovered by De Graaf, hence called *Graafian vesicles*. These contain a serous fluid, with a considerable number of cells, amongst which the ovum lies. In the adult ovary, there are usually from ten to fifty, or more, of these Graafian vesicles, varying in size from a small pin's head to that of a pea. The largest are situated chiefly towards the peripheral part of the organ. In the ovary of the advanced fœtus and new-born child, Graafian follicles are abundant, and, even at this early period, the ovum can be seen within them. The fibrous

stroma of the ovary is exceedingly firm and hard; it consists principally of a modification of white fibrous tissue, the fibres of which interlace in all directions; but it is highly vascular, especially at the period of puberty.

Graafian Follicles.—The *Graafian follicles* or *ovi-sacs* consist, when fully developed, of a closed cavity and contents. The walls are composed externally of a firm fibrous membrane, which is connected with the fibrous structure of the ovary; internal to which is a softer and more spongy tissue, containing numerous fusiform cells and fibres, more loosely arranged than in the external part of

Fig. 263.



Ovary of human subject. *a.* Graafian follicle with opening. *b.* Inner lining of Graafian follicle, or membrana granulosa. *c.* Outer portion of the same. *d.* Ovum. *e.* Vascular wall of follicle. After Coste.

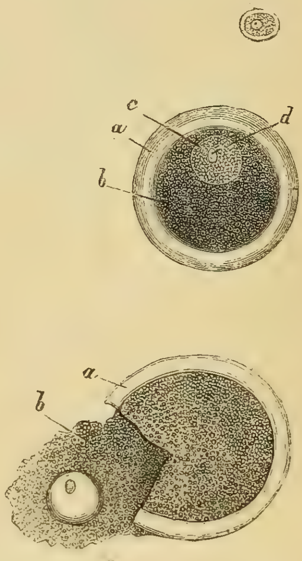
the follicle. Internal to this, especially in young follicles, a clear hyaloid basement membrane may be observed, upon the surface of which, lining the entire follicle, is a tolerably thick layer of epithelium, the *membrana granulosa* of authors. The epithelium is much more abundant in that part of the follicle in which the ovum is situated; indeed, it is entirely imbedded in it. According to the observations of Dr. Barry, the ovum is attached to the walls of the follicle by certain bands, termed by him *retinacula.* It is, however, not easy to demonstrate satisfactorily this peculiar arrangement of the membrana granulosa. The cells of the membrana granulosa of the Graafian follicle have a polygonal form, and immediately around the ovum are collected into a sort of ring,

which is attached to the external clear membrane, or *zona pellucida,* of the ovum. This layer is termed by Dr. Barry, the *tunica granulosa.* The so called retinacula are composed of similar cells, of which many are also found floating in the fluid of the follicle, which is entirely lined by them.

Ovum.—The ovum is invested with a clear, homogeneous, perfectly transparent, firm, elastic, and tolerably thick membrane, exhibiting an appearance, when examined by the microscope, very similar to that of the elastic laminæ of the cornea, the *vitelline* or *yolk membrane,* or *zona pellucida;* the latter being the term always employed in speaking of the mammalian ovum. The zona pellucida appears as a perfectly clear ring, limited on either side by a well defined dark outline. Within this membrane is the yolk, which is composed of a fluid containing proper *yolk granules* and oil particles, with the clear bright *germinal vesicle,* containing within it the *germinal spot,* lying close beneath the zona pellucida.

The ovum is about $\frac{1}{120}$th, and the germinal spot about $\frac{1}{1000}$th to $\frac{1}{800}$th of an inch in diameter.

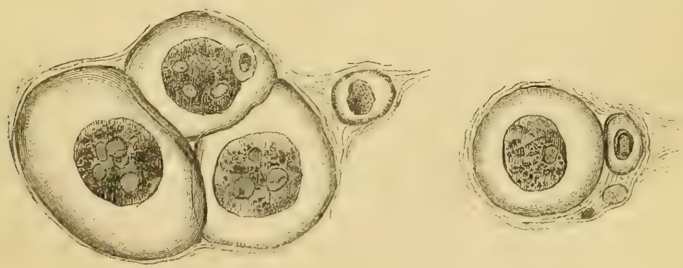
Fig. 264.



Mammalian ova. The upper figure shows an ovum at an early stage of development. The second figure, a mature ovum. *a.* Zona pellucida. *b.* Yolk. *c.* Germinal vesicle. *d.* Germinal spot. The lower figure shows the zona pellucida *a*, ruptured, and the escape of the yolk granules (*b*) and germinal vesicle through the opening. From Coste.

The yolk granules differ much in size and form in different animals. They are much more numerous in

Fig. 265.



Ova in various stages of development, from the toad's ovary. In the right figure some very small ones are observed.

mature ova than in ova at an early stage of development, as was pointed out by Bischoff, an observation which we can fully confirm. They appear to be composed of a protein compound, with much fatty matter.

Germinal Vesicle.—The germinal vesicle, or vesicle of Purkinje, consists of a perfectly clear cell, filled with transparent contents, but containing one dark spot, the *germinal spot.*

From some observations of Kölliker and Bagge upon the development of the ova of intestinal worms, it appears that the germinal spot is the part of the ovum which is first formed; but it may be regarded as a fact, that the germinal vesicle precedes the formation of the yolk and the zona pellucida. The immediate *formative organ* of the ovum is the Graafian vesicle.

As the ovum approaches maturity, it passes from the centre of the Graafian follicle towards its peripheral portion, and becomes imbedded in the membrana granulosa, which increases in thickness until it entirely surrounds the ovum. At the same time, the zona pellucida increases in thickness, and the germinal vesicle, which was originally situated in the centre of the yolk, makes its way towards the circumference.

Parovarium.—Diverging from the hilus of the ovary, may be seen a few canals, which appear to be the remains of the Wolffian body, an organ which reaches its maximum of development in intra-uterine life. These tubes have been termed the *parovarium.*

Fallopian Tube.—The Fallopian tube, or *oviduct,* is a fibro-muscular canal, lined with ciliated epithelium, opening by one extremity into the uterus and terminating in the other by a wide fimbriated orifice, *morsus diaboli,* which opens into the cavity of the peritoneum. Each Fallopian tube is usually, however, connected to the corresponding ovary by one of its fimbriæ.

The Fallopian tube is invested with peritoneum, and at the fimbriated extremity, the serous membrane becomes continuous with its mucous lining. The muscular fibres of the Fallopian tube are disposed in two layers; the external having a longitudinal and the more internal a circular course. The contractile fibres are mixed with much fibrous tissue. The contraction of the oviduct has a vermicular character. The mucous membrane is disposed in longitudinal folds, upon which lies a single layer of columnar epithelium. These cells are ciliated, and by the vibration of the cilia, a current is produced, the direction of which is from the ovaries towards the uterus; so that the transmission of the ovum into the uterus would be favored, while the passage of the spermatozoa along the tube would be retarded.

Uterus.—The uterus is a firm hard body, of a pear shape, flattened more or less anteriorly and posteriorly. On each side, at the upper part, are situated the two angles into which the Fallopian tubes open. The portion above this point is called the *fundus,* while the lower constricted part of the organ is spoken of as the *cervix* or neck, and that part situated between the cervix and fundus is denominated the *body.* The highest part of the neck is spoken of as the *os internum.* The cavity of the uterus is of a triangular shape, about an inch and a half in width at its upper part, where the Fallopian tubes open; but in the unimpregnated state, its walls almost touch each other, so as to leave a very slight interval, which is usually occupied by mucus. The cavity terminates in the *os uteri,* or *os tincæ,* a transverse opening, bounded anteriorly and posteriorly by two thick and rounded lips.

Fig. 266.

Muscular fibre cells, from a gravid uterus, in different stages of development. *a.* Formative cells *b* and *c.* Cells at an advanced stage, from a uterus at the fifth month. The long cell is taken from another uterus at the sixth month. *c.* Its nucleus. After Kölliker.

The uterus undergoes extraordinary alterations in form and size after the impregnation of the ovum, and becomes very vascular and endowed with a highly contractile power.

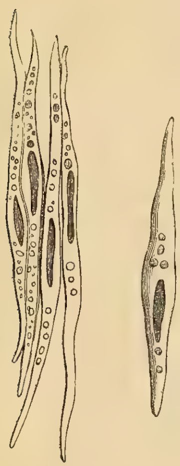
The walls of the unimpregnated uterus are about half an inch in thickness in their thickest part, and consist of pale organic muscular fibres, with a certain quantity of fibrous and areolar tissue. The muscular fibres have been said to be arranged in three layers, but the limits of these

layers are not very clearly defined. The outermost layer is very thin, and is incorporated with the sub-peritoneal tissue. It consists of longitudinal and transverse fibres, many of the latter, after investing the anterior and posterior surfaces of the organ, lose themselves upon the Fallopian tubes, or enter the broad and round ligaments. The middle layer makes up the greater part of the thickness of the uterine walls, and consists of strong bundles; which also run, some in a longitudinal and others in a transverse direction. It is in this layer that the greater number of the vessels which supply the organ, and which become so enormously developed in pregnancy, ramify. The innermost layer is thinner, and composed chiefly of thin longitudinal fibres.

Round the external os uteri, the transverse fibres are very abundant, and collected together beneath the mucous membrane, so as to form a sphincter muscle.

In these different layers, in the virgin uterus, the muscular fibre-cells for the most part are seen as short spindle-shaped cells, in many of which, oval elongated nuclei can be demonstrated. At this period, the cells are often seen to be of very irregular form, and are not always very readily made out. The muscular fibre-cells undergo increased development in the pregnant state, and towards the end of this period, will be found to be very long cells with a distinct oval nucleus. The cell terminates in long thin and pointed extremities (fig. 266). After delivery, these cells again diminish in dimensions, a number of fat globules appear in their interior, and ultimately they regain their former appearance (fig. 267); while, at the same time, the entire organ returns to its former volume.

Fig. 267.



Muscular fibre cells from the uterus, three weeks after parturition, showing the fat globules in their interior. The four cells to the left have been treated with acetic acid. After Kölliker.

The mucous membrane of the uterus forms a pale and not very thick lining membrane. In the fundus and body of the organ, it is of a redder colour than in the cervix, in consequence of the greater vascularity of this part.

The epithelium is of the ciliated variety.

Imbedded in the mucous membrane of the uterus are nume-

rous glandular follicles, much resembling the follicles of Lieberkühn, in the intestine. These follicles are lined with cylindrical epithelium. They appear to form a little whitish mucous secretion. In pregnancy, these glands are enormously developed; and we shall consider the changes taking place in their structure, when describing the alteration which takes place in the mucous membrane of the uterus after conception. The mucous membrane of the cervix uteri is gathered into deep folds, forming *rugæ,* between which are seen secondary rugæ, with a few follicles opening between them. These rugæ were described by the older anatomists, under the terms *plicæ palmatæ, arbor vitæ uterinus*, etc.

In the mucous membrane of the neck of the uterus, are situated the so called *glandulæ,* or *ovula Nabothi,* which secrete the thick mucus usually plugging up this part of the canal. These are closed follicles, and it is probable, that, at certain periods they burst, discharging their contents, and are succeeded by the development of new follicles.

Surrounding the os uteri there are several tongue-like processes of mucous membrane, the villi of the os uteri. Each contains a vascular loop, and is covered with squamous epithelium.*

The nerves of the uterus are derived from the hypogastric plexus. According to Dr. Beck the nerves spread out upon the surface of the uterus itself are few in number, and consist of branches which do not unite with each other so as to form a plexus. Dr. Lee describes numerous ganglia connected with these nerves; and his dissections would appear to show that the uterus is much more abundantly supplied with nerves, than is admitted by anatomists generally. We are not, however, prepared to admit that the textures displayed in the elaborate dissections of Dr. Lee, are entirely or even in great part nervous, or that the bodies which he has represented as ganglia, are really of this nature. This anatomist, like William Hunter, and Tiedemann, considers, that in the gravid uterus the nerves become much increased in size; an opinion which Dr. Beck has failed to confirm in his very careful and elaborate dissections.†

The *ligaments* of the uterus are described in works on descriptive anatomy. They are the anterior and posterior ligaments, the broad ligaments and the round ligaments. The two first being merely folds of peritoneum, the latter a rounded cord about five

* These villi have lately been carefully described by Dr. Tyler Smith, Med. Chir. Trans., vol. xxxv.

† Phil. Trans. 1846, part ii.

inches in length. Mr. Rainey has shown that the round ligament of the uterus contains numerous striped muscular fibres. He describes the round ligament as arising by "thin fasciculi of tendinous fibres; the inner one from the tendon of the internal oblique and transversalis near the symphysis pubis, the middle one from the superior column of the external abdominal ring near to its upper part, and the external fasciculus from the inferior column of the ring just above Gimbernat's ligament."

The fibres pass backwards and outwards, soon become fleshy, unite to form a rounded cord which runs between the layers of peritoneum forming the broad ligament of the uterus, and is inserted into the upper and anterior part of the uterus. The action of these fibres would be to draw the uterus forwards and thus elongate the vagina.*

Vagina, and accessory Female Organs of Generation.—The vagina consists of an external or fibrous layer, and a muscular coat. It is lined by mucous membrane.

The fibrous tissue of the external coat contains many fibres of the yellow elastic element, and a large net-work of vessels, with plexuses of veins which form an erectile tissue.

The muscular fibres run partly in a longitudinal direction, and are partly arranged in transverse bundles which encircle the vagina.

The mucous membrane is of a pale reddish colour, thrown into many small, firm, prominent folds, *columnæ rugarum,* separated by fissures. The epithelium of the vagina is very large, and of the scaly variety. These cells are almost always present in the urine of females. The nucleus is usually seen very distinctly, and is of an oval form. They present examples of the largest epithelial cells in the body. Close to the external orifice, the mucous membrane forms a re-duplication, termed the hymen, which extends across the posterior part of the opening.

There are two small glands, the *glands of Bartholini,* in the female, which correspond to Cowper's glands in the male. They are small branched glands, the ultimate vesicles of which are lined by tesselated epithelium. They appear to secrete a clear yellowish thick mucus.

The corpora cavernosa of the *clitoris* correspond in structure to those of the penis of the male, but are of very small size. Valentin has described helicine arteries, as in the penis. In the mucous membrane of the external female genital organs, are numerous

* Phil. Trans. 1850, part ii. p. 515.

glands; and in the labia majora are some sebaceous glands, opening into the hair follicles, which are so numerous in this region.

The papillæ in this situation are very numerous and highly developed, and are covered with scaly epithelium. The submucous tissue is abundant, loose, and without fat; it contains many fibres of the yellow element. At the labia majora, the mucous membrane becomes continuous with the external skin, to which it gradually approaches in structure.

Urethra.—The female urethra is much shorter and wider than that of the male. It is about an inch and a half in length, and terminates in the *meatus urinarius,* which opens in the vulva between the nymphæ. This canal may be enormously dilated without danger, and a very large calculus has often been extracted from the female bladder through it. The mucous membrane, especially near the bladder, contains many follicles.

Besides the works already referred to in the Notes, the authors recommend the reader to consult the following:—Kölliker's "Manual of Human Histology," translated by Busk and Huxley, Cavendish Society. Dr. Barry's Papers in the Phil. Trans., 1838–40. Dr. Lee's "Memoirs on the Ganglia and Nerves of the Uterus," 1849. Dr. Snow Beck "On the Nerves of the Uterus,' Phil. Trans., 1846. Quain and Sharpey's Anatomy.

CHAPTER XXXIX.

PUBERTY.—MENSTRUATION.—MATURATION AND DISCHARGE OF OVA.—FORMATION OF CORPORA LUTEA.—STRUCTURE OF CORPUS LUTEUM—DISTINCTION OF THE TRUE FROM THE FALSE CORPUS LUTEUM.

THE period of puberty commences at different ages, is characterised by different phenomena, and lasts during widely different periods of time, in the two sexes. In the *male*, puberty seldom occurs before the fourteenth or fifteenth year. It is marked by increased development of the genital organs, the formation of spermatozoa, and the occurrence of sexual feelings. Besides these changes, however, there are others scarcely less striking and characteristic, as the growth of hair on the face and pubes, increased development and symmetry of the limbs and general outline of the body, an alteration in the physiognomy, a greater capacity of the respiratory organs, and a striking change in the character of the voice, which becomes of a deep tone, very different from that of boyhood and of the female sex. This alteration of the voice does not take place in eunuchs, who retain throughout life a shrill tone, of higher pitch, approximating more in character to the female voice than to that of the male. Perfectly-formed spermatozoa are not found in the genital organs of the male before the period of puberty. The power of procreation lasts much longer in the male than in the female, and often continues up to the sixtieth or sixty-fifth years; and instances of virility are recorded at the advanced age of one hundred.

In the human *female*, puberty is likewise characterised by the occurrence of certain local changes in the generative organs, and also by changes of a more general character occurring in the body. About this time, which usually occurs between the thirteenth and sixteenth years, but somewhat earlier in hot climates, the organs of generation undergo a considerable increase in size; the breasts

enlarge, and an increased deposit of fat takes place over the surface of the body generally. The most important indication, however, of puberty, or aptitude for procreation, in the human female, is the appearance of the *catamenia*. Nevertheless, instances have occurred in which the menstrual secretion was retarded for several years, or even in which it never appeared, although the susceptibility for procreation existed, and impregnation had taken place. Hence, although the presence of the menstrual discharge indicates that the period of puberty has arrived, its absence cannot be looked upon as a proof of the want of procreative power; while, in some instances, the catamenia may appear regularly without impregnation ever taking place, in consequence of certain abnormal conditions of the organs of generation. The period of puberty is more affected by the habits of the individual than by temperature, although the latter probably exerts some slight influence. In Africa, menstruation is said to be common as early as the eighth or ninth year; but in colder climates, and in our own country, it seldom occurs before the thirteenth year, and usually not till the fifteenth or sixteenth year. Still cases are on record in which the catamenia appeared in young children in this country; and their appearance was marked by enlargement of the breasts, and other changes indicative of puberty.

In both sexes, the period of puberty is much influenced by the conditions under which the child is placed. Habits of indolence, luxury, and indulgence, tend to the early development of puberty; while, on the contrary, it occurs some years later in those who are inured to active employments, and who are placed under conditions favourable for promoting bodily vigour and mental activity.

The catamenia occur at intervals of a month, and the discharge usually continues from three to six days. It ceases during pregnancy and lactation, and, in most women, does not recur after the forty-fifth to the fiftieth year; but exceptions to these statements are met with from time to time.

At each menstrual period, the mucous membrane of the uterus, and of the generative organs generally, becomes turgid, in consequence of an increased local determination of blood. The mucous surface of the uterus is covered by a sanguineous discharge, which escapes from the turgid vessels.

Of the Menstrual Fluid.—The quantity of the menstrual secretion varies considerably, as also do its characters. In this country, from four to eight ounces are lost at each menstrual period, but sometimes the quantity is much greater. It is of a dark red colour

from the numerous blood corpuscles it contains, and is perfectly fluid, as it is free from fibrine, a character which distinguishes it from ordinary blood. Besides blood-corpuscles, it contains a number of small, pale granular cells, and large corpuscles, containing numerous small oil-globules, the so-called *granular corpuscles.*

Dr. Letheby has published an analysis of menstrual fluid which had accumulated to the extent of forty ounces, in consequence of an imperforate hymen. It was thick and black, and it contained no fibrine. Under the microscope were detected altered blood corpuscles, exudation or granular corpuscles, mucus cells, epithelium, and granules.

Water	857·4
Solid matter	142·6
Fat	5·3
Albumen	69·4
Globuline	49·1
Hæmatin	2·9
Salts	8·0
Extractive matter	6·7

Maturation of Ova, and their Discharge from the Graafian Follicle.—The most important of the phenomena, however, accompanying menstruation, is the maturation and discharge of ova from the ovary. At these periods, a Graafian follicle becomes enlarged, projecting considerably from the surface of the ovary, and distended with fluid. Its wall becomes thin at one point, where it at length gives way, and the contents of the follicle escape into the Fallopian tube. The ovum has but rarely been detected in the Fallopian tube, which is scarcely to be wondered at when we consider its small size, and the very few cases in which we have an opportunity of searching for it with a chance of success. It has, however, been actually seen in one case in the human female examined by Dr. Letheby, and in another by Mr. Hyett. In animals, it may be detected without difficulty, although it is only of late years that the escape of the contents of a Graafian follicle at each menstrual period has been placed beyond a doubt. We owe to Dr. Robert Lee, observations, made so long ago as the year 1831, which establish the fact of the rupture of a follicle, and the escape of its contents, at each recurrence of menstruation. Ova have been detected in the ovaries at a very early age.

Dr. Ritchie states, that, even during childhood, there is a continual rupture of ovisacs and discharge of ova taking place; but it is not until the period of puberty that the number of ovisacs

becomes very great, or the ova are perfectly developed and capable of being impregnated. At this time, the stroma of the ovary is seen to be everywhere studded with ovisacs in various stages of development; the largest and most mature occupying the peripheral parts of the organ, while those containing mature ova, which are about to be discharged, form considerable prominences, projecting from the surface of the ovary.*

The discharge of ova from the ovary in animals, as in the human subject, occurs only at certain definite periods, which vary much in different animals. It is only at these times that the female animal will receive the male, and that the aptitude for conception exists. At such a time the animal is said to be "in heat" or "rut." In the bitch, this period occurs twice in the year, and lasts for about a fortnight each time; in the sheep and in the cow, and in domestic animals generally, it occurs much oftener than in wild animals, and the periods of recurrence are not definite.

If the ovary of an animal be examined at the time of "heat," it will be found turgid with blood, and several Graafian vesicles will be seen projecting from its surface, forming prominences, the most superficial portions of which appear quite thin, and almost ready to rupture and permit the escape of the contents of the follicle. At the same time, a more abundant secretion of mucus takes place from the walls of the vagina and contiguous parts. In a few instances, also, a bloody discharge has been detected in the vagina; but it must be distinctly borne in mind, that this is not a constant phenomenon. It only occurs in small quantity, and it never appears at each successive period of heat, while it is always accompanied with increased sexual desire.

It may be considered as established, that in the human female, at or about the period of menstruation, a discharge of ova takes place; and at these times the ovaries are extremely turgid, and their vascularity is much increased. From very numerous observations, it has been distinctly proved, that conception is more likely to take place a few days after menstruation than at any other period, a fact which has led Naegele to fix the period of delivery at nine months and eight days after the last menstrual discharge; while, in a few instances, the ovum has actually been seen within a very short time after its escape from the Graafian follicle.

From these facts, most physiologists have been led to look upon

* Dr. Barry calculates, that in the ovary of the cow, about the period of puberty, there are as many as two hundred millions, corresponding to a cubic inch of the stroma.

the menstrual periods in the human female as identical with those of heat or rut in animals; a view which has been especially advocated by Bischoff.

The maturation and escape of ova, then, in all animals, is a periodical phenomenon, and even in the human subject, if not accompanied with, is shortly followed by, increased sexual desire; while, in animals, sexual intercourse takes place at these times alone. The rupture of the follicle is probably due to the increased local determination of blood at these periods, by which the contents of the Graafian follicle are forced towards the surface of the ovary. Besides the escape of a certain quantity of blood into the follicle, an exudation takes place from its lower part, so that the contents of the follicle are gradually forced towards the surface, and at the same time, the structures at this point gradually become thinner, until at last the peritoneal coat, and the thin layer of the stroma, give way, and the contents of the follicle escape through the fissure. The opening soon closes, leaving a small *cicatrix*.

After the ovum has arrived at the most superficial portion of the follicle in the manner just described, and is about to escape, the fimbriæ of the Fallopian tube grasp the ovary; and the ovum, after it has escaped from the ruptured follicle, ordinarily falls into the funnel-shaped cavity at the base of the fimbriæ, whence it is transmitted into the Fallopian tube, along which it is gradually propelled, chiefly, no doubt, by the vermicular contractions of the walls, but in part, also, by the vibration of the cilia which line its interior, into the uterus. In some distressing cases, happily very rare, the ovum falls into the cavity of the peritoneum, instead of entering the Fallopian tube, and the embryo becomes developed in this situation. These cases usually terminate in death. Sometimes, however, the remains of the fœtus escape by suppuration through the abdominal walls, or into the intestine.

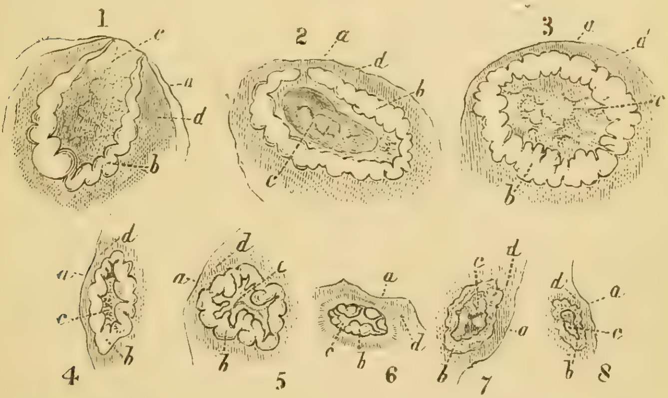
Immediately after the escape of the ovum from the ovary, certain peculiar and characteristic changes ensue in the follicle which contained it, and these are influenced by the occurrence of impregnation. If impregnation has taken place, the lining membrane of the uterus also becomes the seat of peculiar changes, which do not occur under other circumstances. The changes which affect the ovum itself, consequent upon impregnation, will be more conveniently considered when we have referred to the manner in which *corpora lutea* are produced. The mode of formation of the membrana decidua will be alluded to afterwards.

Formation of Corpora Lutea.—If the Graafian follicle of a mam-

malian animal be examined soon after the escape of the ovum, it is found to be almost completely filled with an exudation, similar to that which, by its gradual increase in quantity, has caused the ovum to be carried to the surface of the follicle. In a short time, the outer portion of the follicle is occupied by a firm yellow substance, which is probably formed from plasma, exuded from its walls. After many careful examinations, Dr. Lee has been led to conclude that this yellow matter is deposited external to both the membranes of the follicle.* Montgomery regards it as situated between the layers, while some authorities look upon the internal surface of the inner membrane as the precise seat of its formation. Dr. Zwicky considers the large cells, of which the yellow matter is composed, as modifications of the small cells of the immature follicles. Their nuclei are large and well defined, and they contain numerous oil-globules in their interior. Although bodies, which are liable to be taken for corpora lutea, are, from time to time, found in the virgin ovary, a fœtus has never been found in the uterus without the formation of an unmistakeable corpus luteum Haller's remark, therefore, "nullus unquam conceptus est absque corpore luteo," although made so many years ago, may still be regarded as strictly true.

At first, this exudation is of a dark brown or brownish-red

Fig. 268.



Corpora lutea of the human female at different periods. 1. Eight days after conception. 2. At the end of the second month. 3. At the termination of the fourth month. 4. At the seventh month. 5. Two days after delivery. 6. Twelve weeks after delivery. 7. Corpus luteum of menstruation, or false corpus luteum, four weeks old. 8. Corpus luteum of menstruation thirty days old.

a. Capsule of ovary. *b.* Substance of corpus luteum. *c.* Coagulum occupying cavity in its interior. *d.* Stroma of the ovary.—Altered from figures by Montgomery, Kölliker, and Dalton.

* Med. Chir. Trans., vol. xxii.

colour, resembling effused blood; but soon the colour becomes paler, while its consistence is firmer and more dense. At length the follicle is seen to be occupied with a firm mass, which appears to be formed from a secretion poured out from its walls, which, from its yellow colour in man and many animals, has been called *corpus luteum.* Hence, for every follicle in the ovary from which an ovum is discharged, a corpus luteum will be found. In cases of twins, two corpora lutea are always present; sometimes one in each ovary, sometimes two in one. The characters which the corpus luteum exhibits, and the extent to which the changes giving rise to its formation undergo, will be determined by the circumstance of the ovum being impregnated or not.

Bischoff proved decisively that the ova in mammalia were detached from the ovary at the time of heat, without coition taking place; and that corpora lutea were formed in the ovaries, just as if coition had occurred, and impregnation had taken place.

Raciborski, from numerous experiments upon animals, has shown that whether the rupture of the follicles is or is not accompanied by coitus or by fecundation, the appearance of the lesion which results is, in both cases, absolutely identical.

Nevertheless the corpus luteum of pregnancy, except in its earliest stages, has been admitted by all observers, to possess characters by which it may be distinguished from the corpus luteum formed in a follicle from which an ovum has been discharged without subsequent impregnation having occurred. Hence, *true* and *false* corpora lutea have been described; the true occurring only when conception has taken place, while the false are met with in the virgin ovary. This distinction must undoubtedly be recognised; but there is every reason to believe that the development of a true corpus luteum takes place in obedience to similar nutritive changes which determine the formation of this body, proceeding to a much greater extent than in the case of the false or virgin corpus luteum, in consequence of their being promoted by the increased determination of nutritive pabulum and the greater vascularity of the ovaries when impregnation has occurred.

In the cow (according to Dr. Dalton), the corpus luteum reaches its maximum of development in about two weeks after the rupture of the vesicle, and in three weeks more all that remains is a small yellowish spot. If, on the other hand, the rupture of the follicle be followed by impregnation, the corpus luteum does not attain its greatest size till about the middle of the seventh month, and at the termination of the eighth month it is still of large size, and

sometimes forms a very remarkable prominence on the surface of the ovary.

The corpus luteum of menstruation is smaller than that following conception; its yellow colour appears very rapidly, and soon fades. In the course of one or two months, after their first appearance, they are no longer to be distinguished. Virgin corpora lutea are not vascular, and cannot be injected.

If a section of the corpus luteum be made, a small cavity will be found in the interior, from which several lines appear to radiate towards its external surface. This little cavity gradually contracts, and ultimately disappears. According to Dr. Montgomery, within the first three or four months of pregnancy, the cavity is large enough to contain a grain of wheat, and often much larger. The same observer has always found the cavity absent after the sixth month; usually it seems to disappear between the fourth and fifth months. A few months after delivery, the corpus luteum entirely disappears. Dr. Montgomery never saw one later than the end of the fifth month after delivery.

In a medico-legal point of view, the characters of the corpus luteum are sometimes of great importance, and it will be well to recapitulate the most important. The true corpus luteum of pregnancy possesses very well marked characters, by which it may be distinguished from the false corpus luteum.

Its projection from the surface of the ovary; its large size, often equal to that of a mulberry, and its rounded form; the triangular depression and cicatrix upon its surface; the little cavity in its centre during the earlier period of its formation, or the stellate cicatrix during the latter part of pregnancy; its lobulated or puckered appearance; its firm consistence and yellow colour; its great vascularity, as may be shown by injection, and its persistence for some time after delivery, are all important points in which the *true corpora lutea* contrast remarkably with those which are formed where conception has not taken place. The *false corpora lutea* are small in size, and do not project from the surface of the ovary; they are often angular in form, seldom present any external cicatrix, contain no cavity or stellate marking in the centre; the material of which they are composed is not lobulated, and their consistence is usually very soft; they often resemble coagulated blood; the yellow material exists in the form of a very thin layer, or, as is more commonly the case, not a trace of this substance is present. False corpora lutea are easily broken down, and often consist either of small cysts, containing serum, or of a simple coagulum.

The following works and monographs may be consulted upon the subjects treated of in chapter xxxix : — Dr. W. Hunter on the "Gravid Uterus", 1794. Sir Everard Home, in the Phil. Trans., 1817. Dr. R. Lee's article, "Ovary," in the Cyclopædia of Practical Medicine, 1834 ; and his Lectures on the Theory and Practice of Midwifery, 1844. "An Exposition of the Signs and Symptoms of Pregnancy," etc., by W. Montgomery, M.D., 1856. Dr. Ritchie's Papers in the Medical Gazette, vol. xxxvi. Bischoff, "Beweis von der Begattung unabhängiger Periodischen Reifung und Loslösung der Eier;" Giessen, 1844. Raciborski : "Comptes Rendus," 1843. "De la Puberté et de l'Age critique chez la Femme et de la Ponte Périodique," Paris, 1844. M. Pouchet, "Théorie Positive de l'Ovulation Spontanée," 1847. Müller's Physiology, supplement by Dr. Baly. Dr. Paterson's Papers in the Edin. Med. and Surg. Journal, Nos. 142 and 145. Mr. Roberton's "Essays on Menstruation, and on Practical Midwifery," 1851. Zwicky : "Die Metamorphose des Thrombus;" Zurich, 1845. Prize Essay on the "Corpus Luteum of Menstruation and Pregnancy," by John C. Dalton, Jun., M.D., Philadelphia, 1851.

CHAPTER XL.

IMPREGNATION OF THE OVUM.—CHANGES IN THE OVUM IMMEDIATELY SUCCEEDING IMPREGNATION.—ROTATION OF THE YOLK.—CLEAVAGE OF THE YOLK.—KÖLLIKER'S OBSERVATIONS.—FORMATION OF BLASTO-DERMIC VESICLE, OR GERMINAL MEMBRANE. — FORMATION OF DECIDUA. — STRUCTURE OF THE MEMBRANA DECIDUA. — DECIDUA REFLEXA.

Impregnation of the Ovum. — It is exceedingly difficult to give a satisfactory description of the nature of the phenomena occurring in impregnation. It was recently held, by Mr. Newport and other observers, that the contact of the spermatozoa with the exterior of the ovum was sufficient to impregnate it. It was supposed, that liquefaction of the spermatozoa occurred, and that the solution thus formed permeated the vitelline membrane, and impregnated the ovum. The latest researches, however, of the same indefatigable investigator upon the ovum of amphibia, and upon the mammalian ovum, have demonstrated satisfactorily that the spermatozoa actually penetrate and pass through the yolk membrane, and are thus brought into contact with the yolk in the interior. This view was advocated by Dr. Barry several years ago (in 1843), and its accuracy has since been confirmed by the observations of Newport and Bischoff, and also by Meissner.

What becomes of the spermatozoa when they have reached the interior is unknown. They disappear, and become liquefied; but the precise manner in which this occurs has not been determined, neither is it known if they penetrate far into the substance of the yolk.

Micropyle.—In many ova the vitelline membrane is very firm and hard; and it may be fairly asked, how can the delicate spermatozoa perforate so tough a structure as the investing membrane of the yolk undoubtedly is in these ova? Much light has very lately been thrown upon this part of the process of impregnation by the researches of our friend, Dr. Ransom, of Nottingham, by those of Professors Müller and Remak upon the impregnation of the ova in fishes, and by the investigations of Leuckart, Leydig, and Meissner, upon the eggs of insects, mollusks, and some of the radiata.

These researches establish the fact of the existence of one or more pores or tubes passing through the coriaceous envelope, and opening upon its interior. Leuckart has shewn that these pores are characteristic of all insect ova.*

In July, 1854, Dr. Ransom made some very important observations upon the ova of the stickleback, and demonstrated the existence of a funnel-shaped depression, pierced by a canal, which passes through the chorion in the unimpregnated ovum. This is the *micropyle,* through which the spermatozoa pass to the interior of the ovum. "In the act of impregnation, one or more (as many as four have been seen) spermatozoids pass into the micropyle. Actively moving spermatozoids may remain in contact with the chorion for eighteen minutes at least without producing any sensible change in the ovum, provided none of them enter the micropyle; but when one is seen to enter, in about a quarter of a minute a change is observable."†

Dr. Ransom has found the micropyle in all the fresh-water fishes which he could obtain.

The existence of the *micropyle* in the mammalian ovum has not yet been satisfactorily proved. Remak, however, regards certain streaks existing in the zona pellucida as pores or micropyles through which the spermatozoa may pass.

Changes in the Ovum immediately succeeding Impregnation.—The period of time, at which the ovum leaves the ovary, and passes into the Fallopian tube, varies considerably in different animals; sometimes it occurs within a few hours after impregnation, while in other instances, days, or even weeks, may elapse between the time of coitus and the escape of the ovum from the Graafian follicle. In the dog, the ovum may sometimes be found in the Fallopian tube within thirty-six hours after coitus, and, at others, not until ten or twelve days afterwards. In the roe-deer, four months are said to elapse between the act of impregnation and the escape of the ovum, according to the observations of M. Pockels. About the time that the ovum leaves the ovary, the cells of the membrana granulosa immediately surrounding it undergo a curious change of form, becoming club-shaped; their pointed extremity being attached to the zona pellucida, by which a stellate appearance is produced (fig. 271, B). Each cell contains a nucleus; and the ovum, with these radiating cells, presents a stellate appearance. The cells afterwards become round, and disappear about the time

* Müller's Archiv., 1855.

† Proceedings of the Royal Society, vol. vii. No. 7, Nov. 23rd, 1854.

that the ovum reaches the uterus, except in the case of the rabbit, where Bischoff has observed that they are lost as soon as it enters the Fallopian tube.

Soon after the escape of the ovum from the follicle, and, in some instances, even before this, the germinal vesicle disappears. According to the observations of some observers, amongst whom may be mentioned Barry and Wagner, the germinal vesicle is the seat of cell-formation.* The nature of the earliest changes, however, are very obscure. Eventually, two cells result, which are destined to undergo subsequent division and subdivision.

As the ovum passes along the Fallopian tube, it increases somewhat in size: the yolk becomes of firmer consistence, and shrinks a little, so as to leave a cavity between it and the zona pellucida, which is occupied with a clear fluid. The original vitelline membrane itself, according to Dr. Barry, disappears by liquefaction. The external investing membrane seems to be derived from the mucous membrane of the Fallopian tube, and it is this which at length becomes developed into the chorion.

Dr. Ransom describes the changes in the yolk immediately resulting from impregnation, in the stickleback's egg, as follows:—"About fifteen or twenty minutes after impregnation, a remarkable and more vivid contraction begins, causing the yolk to pass through a series of regularly recurring forms. The contraction begins on one side, near the equator, and soon forms a circular constriction, which gives the yolk the figure of a dumb-bell, the longer axis of which is the polar axis of the egg. The constriction travels towards the germinal pole, and next produces a flask-shaped figure; this is at length lost by the constriction passing on, and the round form is regained in about a minute. This wave re-appears, and travels forward again, without any distinct period of rest; and I have seen these movements continue for forty-five minutes, though towards the latter part of this period they are less distinct and more limited in extent. The germinal mass itself, during these contractions, which strongly resemble the peristaltic movements of the intestine, undergoes changes in form, and has increased in bulk and distinctness. These movements are unaffected by weak galvanic currents. Cleavage begins in about two hours after impregnation: no embryonic cell was observed before it began, nor in any of the cleavage masses."

Rotation of the Yolk.—At a very early period after impregnation, Bischoff has observed, in the ovum of the rabbit, guinea-pig, and some other animals, the very interesting phenomenon of the rotation of the yolk. The movements were of a regular rotatory

* J. Müller has shewn that in *Entochoncha mirabilis* (one of the mollusca), the germinal vesicle does not disappear, but forms the origin of the embryonic cell in the centre of the yolk.

character, and were produced by the active vibration of exceedingly delicate cilia, which had become developed upon the surface of the yolk. This interesting movement may be observed in the ova of frogs and other animals. It can always be seen in those of the common water-snail (*Limnæus stagnalis*), and forms a most interesting object for observation.

Cleavage of the Yolk.—Soon after the ovum has become impregnated, and the germinal vesicle has disappeared, the yolk of the mammalian animal divides into two large cells, and each of these again subdivides into two, so that the yolk mass now consists of four cells, which soon become sixteen in number; these sixteen, thirty-two; and so on, until at last the yolk consists of an aggregation of spherical cell-like bodies. Each one of these, in the mammalian ovum, is about the 1-2000th of an inch in diameter, and consists of a central light portion, and an external dark part. The external part, which is composed entirely of yolk granules, is not covered by an investing membrane, but the yolk granules seem to be simply aggregated round the central clear vesicle, which, when set free, looks very like an oil-globule. According to Bischoff, this vesicle cannot be looked upon in the light of a nucleated embryonic cell. It is probably more correctly considered as a nucleus, around which yoke granules have become attracted.

The process of cleavage of the yolk is very easily observed in the eggs of the batrachia (frogs, newts, etc.), in which animals the change may be watched from day to day. The division of the yolk has been also very carefully investigated in the ova of certain entozoa, in different species of which two distinct modes of division have been demonstrated.

Kölliker found in the ova of certain species of *Ascaris* (*nigrovenosa, acuminata*, and *succisa*), that after the disappearance of the germinal vesicle, a new nucleated cell appeared in the centre of the yolk, and in a short time two such cells manifested themselves. Round each one of these cells portions of yolk-mass collected, so that soon the entire yolk was divided into

Fig. 269.

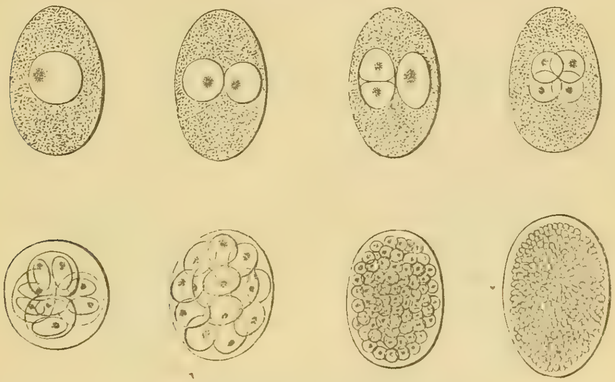
Cleavage of the yolk in Ascaris nigrovenosa and acuminata, shewing successive steps of the process of yolk-cleavage. The three figures to the left are after Kölliker, the two others after Bagge.

two parts, in the centre of each of which a nucleated cell was situated. Each of these cells again subdivides, and corresponding portions of the yolk surround the cells resulting from the original sub-division. This process continues to be repeated until at last the individual cells cannot be distinguished, and a granular mass results, from which the young worm is gradually evolved. The division of the yolk appears to result from an attraction existing between its particles and the cells, which divide previous to the subdivision of the yolk-mass.

In the *cephalopoda*, only a portion of the yolk undergoes subdivision, the remainder serving for the nutrition of the embryo during incubation ; hence the division into *germ-yolk* and *food-yolk*. Amongst the vertebrata, this type is followed in the class of fishes and birds, and in many reptiles.

In the development of the ovum of *ascaris dentata*, Kölliker has found that a totally different process occurs. In this entozoon, the first embryonic cell is developed in the centre of the yolk after the disappearance of the germinal vesicle, and grows at the expense of the yolk substance, instead of causing

Fig. 270.



Multiplication of cells in the yolk. The first four figures, are ova of Ascaris dentata ; the remainder, of Cucullanus elegans. After Kölliker.

the latter to collect around it. This cell divides into two, which appropriate nutriment in the same manner ; and further division and subdivision occurs, until at last the yolk entirely disappears, and its place is occupied by a number of cells, resulting from the division of the primary cell, and the absorption of the yolk-mass by the subsequent cells.

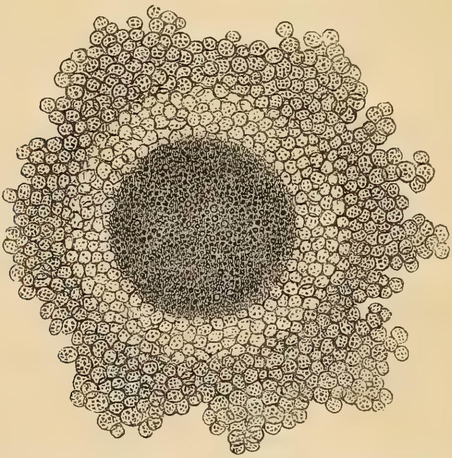
Among the invertebrata, therefore, we have seen three distinct types upon which the division and subdivision of the yolk occurs ; but in all we notice the disappearance of the germinal vesicle, and the formation of a new "embryonic" cell, by the division of which a large number of cells is at length produced, giving the ovum the appearance of being composed of a *granular mass*, from which the embryo is at length formed.

In the mammalia, it is the first of these three modes which is followed. The entire yolk divides, its particles collecting themselves round cells resulting from the division of the embryo-cell, until the yolk-membrane appears to be entirely occupied by granular contents ; in this stage it is often termed the "mulberry mass."

Formation of Blastodermic Vesicle, or Germinal Membrane.—About the time that the ovum reaches the uterus, the segmentation is complete, and in its general appearance it much resembles the ovarian ovum; but according to Bischoff, upon careful examination, it is found that the apparently granular mass is really aggregated into minute spherical masses, in the centre of each of which is situated a clear vesicle. Soon each of these collections of granules becomes surrounded with an investing membrane, so that cells are formed, the nuclei of which are represented by the clear central vesicle. The more peripheral cells are first formed, and these from mutual pressure assume a pentagonal or hexagonal form; they become flattened, and united together at their margins, like pavement epithelium. The same process takes place in the interior of the yolk-mass, and as the cells are formed they pass towards the surface, and thus the thickness of the layer first produced becomes increased. A clear fluid only occupies the central part of the yolk. Thus, after the termination of the cleavage process, a membrane composed of cells is formed within the zona pellucida, which Bischoff has termed the "*blastodermic vesicle.*" Soon after the formation of this membrane, but not until it has increased in thickness by the addition of new cells upon its inner surface, formed from the contained yolk-mass, an opaque roundish spot, consisting of cells and nuclei, makes its appearance at one spot.

Fig. 271.

A

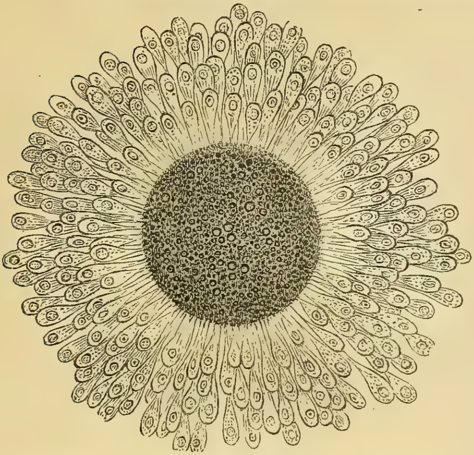


Ovum from the ovary of the Guinea-pig, surrounded by the membrana granulosa, through which the zona pellucida is distinguished.

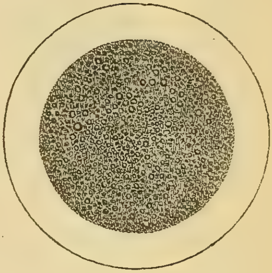
Fig. 271.

Earliest changes in the mammalian ovum, consequent upon impregnation.

B



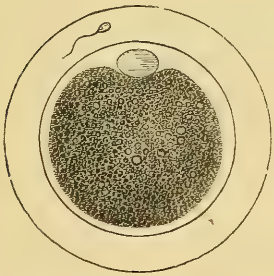
A perfectly mature ovum from the ovary, showing the spindle-shape which the cells of the discus proligerus have assumed.



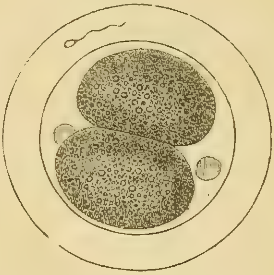
C

The same ovum with the cells of the discus proligerus removed. The germinal vesicle has disappeared.

D



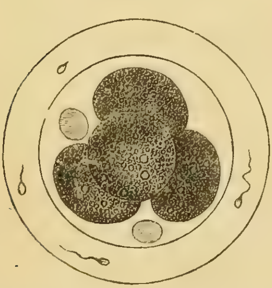
An ovum from the upper third of the ovary. The yolk does not completely fill the cavity of the zona pellucida. Between it and the zona is seen a clear transparent body, distinct from it. Rotation of the yolk was visible in this ovum.



E

An ovum from the middle of the ovary. The yolk is divided into two masses. Two clear vesicles are seen between it and the zona. A spermatozoon is observed upon the zona pellucida.

F



The yolk divided into four portions. This ovum was taken from the lower third of the ovary.

G

An ovum from the upper part of the uterus, four days old. The segmentation of the yolk has proceeded still farther.

Fig. 271.

II

I

An ovum also from the upper part of the uterus, showing the further subdivision of the yolk; but the separate portions are beginning to become incorporated.

An ovum from the upper part of the uterus, on the sixth day. The yolk-masses have become incorporated into a single mass, which does not entirely occupy the cavity of the zona pellucida.

All the ova delineated in Fig. 271 have been copied from Bischoff's beautiful Memoir on the Development of the Guinea-pig. Giessen, 1852.

It is in this space, or "*area germinitiva,*" that the first traces of the embryo appear; and it is developed upon the surface of the "germinal membrane," or "blastodermic vesicle," being covered only by the zona pellucida. As occurs in the bird's egg, the germinal membrane soon becomes divided into two layers: an *external* or "*serous layer,*" or *animal layer*, in which the brain and nervous system and different organs of animal life are developed; and an *internal* "*mucous*" or *vegetative layer,* from which the alimentary canal and organs of vegetative life take their rise.

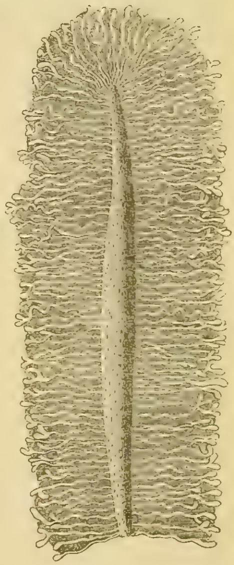
At the same time that these changes are taking place in the interior, the albuminous layer on the external surface of the ovum coalesces with the zona pellucida, forming a single membrane, from which the chorion is formed, or, as maintained by Dr. Barry, the zona pellucida is first removed, and a completely new investing membrane produced.

Formation of Decidua.—Besides the changes which occur in the ovum immediately after conception, which result in the formation of the embryo, and the development of a new covering termed the *chorion* upon its external surface, alterations of another order are taking place in the uterus, by which its internal surface becomes adapted for providing nourishment for the embryo in its very early stages, before it has reached that period of development when it is enabled to derive its nutriment by direct absorption from the blood of the mother. The change in question consists in the for-

mation of a soft pulpy tissue, containing cellular elements in great abundance, over the whole internal surface of the uterus. In this soft spongy substance the ovum becomes imbedded, and with it the chorion becomes intimately connected. This membrane, in consequence of its being thrown off at each parturition, has been termed the "*membrana decidua*."

The decidua was formerly looked upon as an *exudation* from the mucous membrane of the uterus; but from the observations of Professor E. H. Weber and Dr. Sharpey, it has been shown to consist of the much thickened and altered mucous membrane itself. It appears to be composed of glands lined with epithelium, between which ramify vessels surrounded by much soft pulpy tissue, composed principally of nucleated cells. At the time of its formation, the ordinary ciliated epithelial lining of the unimpregnated uterus entirely disappears, and its cavity soon becomes filled with a fluid secreted by the soft and swollen decidua. The os uteri is plugged up by a soft, viscid, mucus-like mass, composed of a secretion from the decidual membrane; but the cells which are found in it differ materially in character from those immediately surrounding the ovum, in being of an elongated form, while the latter are spherical, and, according to Professor Goodsir, perform the very important office of elaborating the nutrient material for the ovum.

Fig. 272.

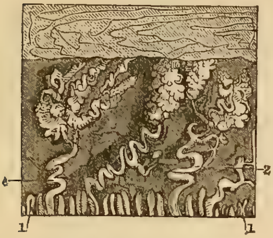


Section of human uterus at commencing pregnancy, showing the glands in the mucous membrane, and their openings. Twice the natural size. After Weber.

Structure of the Membrana Decidua.—In the unimpregnated uterus of the bitch and other animals, and probably also in that of the human subject, but more minute, are situated numerous small glands, which increase enormously in size immediately after conception. In the human uterus, soon after impregnation, they are seen as elongated wavy tubes, having a tolerably straight course in their more superficial part, but much contorted towards their deep aspect, where they terminate in two or three cœcal extremities. The space between these tubes, contains capillary vessels and numerous cells, to the increased development and multiplication of which, according to Professor Goodsir, the greatly increased thickness of the mem-

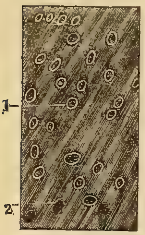
brane is due. In the mucous membrane of the uterus of the bitch, Dr. Sharpey has described two distinct kinds of glands, one simple and the other compound. The openings of both these forms of glands may be readily seen upon the surface of the mucous membrane; and they soon increase in dimensions, in order to receive the fœtal processes of the chorion, which are covered with epithelium, similar to that lining the follicle. Immediately before the large compound glands open upon the surface, Dr. Sharpey describes their tube as forming a dilatation or cell, into which a fœtal process of the chorion is received. At the bottom of this cell the duct may be seen; and as it passes towards the deep surface, it is observed to form the branched compound gland. At parturition, the vessels of course come away with the decidual membrane, as well as the cells just referred to, but the ducts and branching terminations of the glands remain behind. From this arrangement it follows that, in the bitch, the secretion elaborated from the system of the mother by the agency of these glands is brought into close contact with the vessels of the fœtus, and afterwards absorbed by them.

Fig. 273.



Uterine glands of the bitch. Twelve diameters. 1. Simple glands. 2. Compound glands. After Dr. Sharpey.

Fig. 274.



Thin section of human decidua soon after impregnation had taken place, showing glands divided transversely. Magnified twelve diameters. 1. Tube with epithelial lining. 2. Tube from which the epithelium has escaped. After Dr. Sharpey.

In the human decidua, the openings of the glands may be distinctly seen, and their epithelial lining readily traced. The tubes can be followed through the membrane; in fact, from numerous observations, there can be no doubt that, like the decidual membrane in the bitch, the human decidua consists really of the altered mucous membrane of the uterus.

Leydig has seen ciliary motion in the uterine glands of the sow.

Next we have to consider how it is, that the ovum becomes covered with the decidual membrane. Dr. W. Hunter looked upon the decidua as a closed sac, separating the uterine cavity from the openings of the Fallopian tubes. When the ovum descended, he supposed that it pushed the decidua, as it were, before it, and thus became covered, in the same manner that the viscera are invested with peritoneum; and hence, Dr. Hunter termed that portion of decidua covering the ovum, *decidua reflexa*, while that lining the uterus was

called *decidua vera.* As the ovum increased in size, that part of it towards the Fallopian tube, which of course remained uncovered by the reflexa, at length received a covering, which was termed *decidua serotina.*

Decidua Reflexa.— Since the time of Dr. W. Hunter, much difference of opinion has arisen among anatomists as to the manner in which the ovum became covered with decidual membrane. That his view was incorrect, follows from the fact which has been ascertained by subsequent researches,— namely, that the decidua itself consists of the altered mucous membrane of the uterus, and therefore, like it, is *continuous* with the mucous lining of the Fallopian tubes, and not stretched across the opening, so as to be pushed forwards by the ovum in its descent. The structure of the decidua reflexa, as was pointed out by Goodsir, differs from that of the vera in not containing many ducts. It does, however, contain a few, which are derived from that part of the decidua vera which is continuous with it.

Dr. Sharpey considers the central part of the decidua reflexa as formed by a layer of exuded lymph, with which the ovum is covered upon its entrance into the uterus, and that the decidua vera extends upwards around it to a point where these two structures become continuous. He also offers the more simple suggestion, that the ovum may first become completely imbedded, and then may carry forward with it a covering of the membrane as it increases in development. A view which agrees in the main with Dr. Sharpey's, and which is probably nearest the truth, is that of M. Coste, who supposes that the ovum becomes partially imbedded in the decidual membrane and soft pulpy matter poured out by its glands. As the ovum increases in size, the decidua grows up around it, so as ultimately to cover it completely.

The two layers of decidua above referred to, gradually come in contact as the ovum increases in size, until, towards the end of the third month, they are incorporated together and form one membrane, which becomes thinner as pregnancy advances, and is expelled with the fœtus at the termination of the period of gestation.

The decidua is a structure admirably adapted for the ovum to be imbedded in in the early stages of its existence, and the numerous glands in its substance seem evidently destined to elaborate a pabulum fitted for its nutrition, before its own especial organs are sufficiently advanced in development to select and absorb the materials for its subsistence.

The tufts or villi of the chorion, each of which consists of a collection of nucleated cells within a delicate membrane, are the organs by which this nutriment is at first absorbed, just as the collections of cells at the terminations of the minute divisions of the root of the plant absorb and appropriate nutriment from the soil. Soon, however, vessels are prolonged from the fœtus into these tufts, and thenceforward it continues to be nourished from the vascular system of the mother; but the nutrient matter is still transmitted through the layer of cells covering the vascular maternal surface, as well as that covering the fœtal tuft. The precise nature of this arrangement we shall have to consider when discussing the mode of formation of the placenta.

Upon the subjects discussed in chapter xl., the reader is referred to the following works and monographs, besides those mentioned in the notes:— Mr. Newport, "On the Impregnation of the Ovum in Amphibia," Phil. Trans. 1851-53; Dr. Barry's "Researches in Embryology," Series I., II., III., in Phil. Trans., 1838-40; Dr. Sharpey, "On the Structure and Functions of the Membrana Decidua and the Uterine Glands," in Müller's Embryology, translated by Dr. Baley; "De Evolut. Strongyli Auric. et Ascarid. acum. Vivip.," Diss. Inaug. Erlangæ, 1841; Bischoff, "Entwickel. des Hundeeies"; Vogt, "Untersuchungen über die Entwickelung der Geburtshelfer-kröte Solothurn," 1841; Goodsir's "Anatomical and Pathological Observations;" M. Coste, "Comptes Rendus," 1847; Dr. Ransom, "On the Impregnation of the Ovum in the Stickleback," in the Proceedings of the Royal Society, vol. vii. No. 7, 1854; Leuckart, "On the Micropyle and Minute Structure of the Egg-shell in Insects," Müller's Archives, 1855.

CHAPTER XLI.

ON THE DEVELOPMENT OF THE EMBRYO—EARLY CHANGES IN THE BIRD'S OVUM—AREA PELLUCIDA, AREA GERMINITIVA, AREA VASCULOSA—SEROUS AND MUCOUS LAMINÆ—INVESTING MEMBRANE AND MEMBRANA INTERMEDIA OF REICHERT—CHANGES IN THE MAMMALIAN OVUM—PRIMITIVE STREAK—FORMATION OF DORSAL AND VENTRAL LAMINÆ—FORMATION OF THE AMNION—BRANCHIAL FISSURES AND ARCHES—HEART AND LARGE ARTERIES—ALLANTOIS—DEVELOPMENT OF THE HUMAN EMBRYO.

In the last chapter we described the earliest changes resulting from impregnation, and traced them up to the formation of the germinal membrane, and the first appearance of the embryo. We have now to consider the manner in which the development of the embryo takes place, and the mode in which the different organs are evolved. It will be most convenient to describe, as briefly as possible, the earliest changes occurring in the bird's egg, in the first instance, and then to consider the development of the mammalian ovum, and that of the human subject.

Early Changes in the Bird's Ovum.—In considering the nature of the earliest changes in the egg, resulting from impregnation, but which are dependent for their commencement and continuance upon a temperature varying from 95° to 104° F., we must premise that the yolk of the bird's egg consists of two distinct portions, one which undergoes segmentation, and alone takes part in the formation of the embryo—*the germ-yolk;* the other, and by far the larger portion, does not undergo segmentation, and takes no part in the formation of the germ, but provides the pabulum for its development and nutrition, whence it is termed the *food-yolk.*

Area Pellucida, Area Germinitiva, and Area Vasculosa.—A few hours after the egg has been exposed to a hatching heat, it will be found that the *germ* has become less adherent to the vitelline membrane. It has assumed a more membranous appearance; and about the sixth or seventh hour, a clear space may be discerned in its centre.

This increases gradually, until it is about a line in diameter. It is called the *area pellucida*. The darker and more granular part, external to the area pellucida, is the *area germinitiva*, in which may be observed a darker portion, which is the future *area vasculosa*, so called, because vessels are first observed in this situation. The germinal membrane is composed entirely of cells, which result from the original process of cleavage (page 574). These cells increase at its margin; and in this way the germinal membrane gradually extends itself so as to invest the entire yolk.

Serous and Mucous Laminæ.—At an early period, the germinal membrane manifests a tendency to split into two layers. These are termed *laminæ*. The upper one, which, in its extent, corresponds to the area pellucida, is the *serous laminæ*. The lower one, which is more extensive, and which extends beyond the vascular area, is called the *mucous laminæ*.

Reichert, however, in his beautiful investigations upon the development of the chick, has described the formation of the layers from which the different organs are evolved in a somewhat different manner.

The "Investing Membrane," and "Membrana Intermedia," of Reichert.—The most superficial layer of cells of which the germinal membrane is composed, which is usually known as the "serous layer," has been termed by Reichert the *investing membrane*. It extends, at its circumference, between the yolk and the vitellary membrane by the apposition of new cells of the yolk to its periphery, and is formed independently of the vascular system. The rudiments of the nervous system are first seen in the form of a line (primitive streak) immediately beneath the investing membrane, and are developed from a stratum of cells which has separated itself from the surface of the yolk. Immediately beneath this is another layer of cells which has been termed the mucous layer of the germinal membrane, also the vascular layer, but Reichert has well described it under the term *membrana intermedia*. It is beneath the central organs of the nervous system, and in contact with the chorda dorsalis Lying between the *nervous centres* on the one hand, and the *mucous membrane* on the other; and extending beyond the limits of the *area pellucida*, the *membrana intermedia* gives origin to the *vertebral, cutaneous*, and *vascular* systems, and to the *digestive* system with the exception of its mucous membrane. In the development of the higher vertebrate animals, according to Dr. Reichert, the membrana intermedia performs a most important part.

About the sixteenth hour, between the external and internal layers of the germinal membrane a new deposition of cells takes place, from which the first traces of vessels are produced. This is the *middle* layer of the germinal membrane, commonly known as the *vascular layer*. The vessels are not formed, in the first place, close to the embryo, but at some distance from it, outside the area pellucida, so that now the area pellucida is surrounded by the area vasculosa; and this again by the *area vitellina*. As the vessels increase in number and size, they spread outwards over the area vitellina, and inwards over the area pellucida, until they join the large trunks connected with the heart. A little earlier than this, about the fourteenth hour, in the central part of the long axis of the clear oval area pellucida, which lies in the transverse axis of the egg, appears a line thicker at one extremity than the other. This is the *first trace* of the embryo, and is called the *primitive streak* or the *nota primitiva*.

Fig. 275.

Portion of germinal membrane about the sixteenth hour of incubation. *a*. Germinal membrane. *b*. Area vasculosa. *c*. Area pellucida. *d*. Nota primitiva or embryo.

About the third day of incubation, on each side of the primitive streak, appear two ridges or crests, which are termed *laminæ dorsales*. These gradually arch over, and at length enclose the brain and cord. The chorda dorsalis occupies a position underneath the spinal cord, and appears as a thin gelatinous thread, which corresponds to the axis of the bodies of the vertebræ, which latter, however, are not formed from the chorda dorsalis, but are developed from a double row of four-sided white spots, or *vertebral plates*, arranged symmetrically on each side of the central chorda dorsalis. Passing downwards from the dorsal laminæ, on each side are the *ventral laminæ*, which tend to enclose a space below the corda dorsalis, like that enclosed by the *dorsal laminæ* above it. The former contains the large vessel of the trunk (Fig. 277). The latter the central organs of the nervous system. In this way are produced the *hæmal arch* and the *neural arch* of the vertebræ.

Soon the embryo, and that portion of the germinal membrane immediately connected with it, become somewhat raised; the

embryo itself taking the form of a boat with its concave surface downwards. This is the first appearance of a visceral cavity, bounded by the ventral laminæ, in which the ribs and the transverse processes of the vertebræ are formed.

That part of the most superficial layer of the germinal membrane, or *serous lamina*, immediately surrounding the embryo, forms a prominent fold which soon rises above the surface. According to Reichert, however, the fold is *formed* from the most superficial layer of the *membrana intermedia,* and is only covered by the investing membrane. Each fold approaches that on the opposite side, until, by their approximation and communication, a shut sac is formed, into which fluid is poured. In this fluid, the embryo floats. Its open ventral surface gradually becomes closed, until at last it is connected with the yolk only by means of a very narrow pedicle or cord (*umbilical cord*), which consists of a narrow tube passing from the intestine to the yolk, with certain vascular trunks, through which the nutritive matter absorbed by the vessels ramifying upon the surface of the yolk is carried to the embryo. Of this attenuated cord connecting the embryo with the yolk sac or *umbilical vesicle* we shall speak at some length hereafter. Thus is formed the amnion to which we shall have to allude more particularly in Chapter XLIII.

Such are some of the most important changes occurring during the earliest period of incubation in the chick. We shall now consider the nature of those which take place in the mammalian ovum.

Changes in the Mammalian Ovum.

The essential changes which manifest themselves in the early period of the development of the mammalian embryo are very similar to those which we have briefly described as occurring in the bird's egg; but in consequence of the small amount of yolk in the former compared with the latter, and therefore the greater dependence of the embryo for its nutrition upon external sources, certain differences are observed in the development of the mammalian ovum.

It has been already stated (p. 574) that by the time the mammalian ovum has reached the uterus, the process of segmentation is complete. It is also paler and more transparent. The germinal vesicle had disappeared previous to segmentation;

but whether its contents become mixed up with the substance of the yolk, or new cell-formations primarily result from it, has not yet been conclusively determined.

By the aggregation of cells upon the surface of the yolk, a sort of membrane, composed of pentagonal cells with nuclei is formed within the *zona pellucida*, or yolk-membrane. This is called the *blastodermic* vesicle, and in its mode of formation nearly corresponds to the germinal membrane of the bird's egg.

The *chorion*, or outermost membrane investing the ovum, is formed by the gradual coalescence of the zona pellucida, and the layer of albuminous material with which it is covered. The chorion is at first smooth, but villi are subsequently developed all over its surface. Beneath the chorion is the blastodermic vesicle, which gradually increases in thickness by the growth of new cells upon its internal surface.

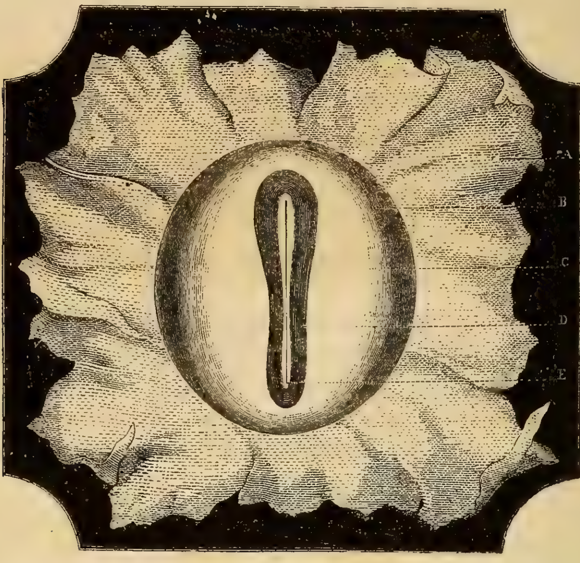
In consequence of the great difficulty experienced in procuring human ova at a very early period in a perfectly normal state, and in sufficient number, physiologists have been compelled to make direct observations upon the lower animals, and to assume that a series of changes precisely similar takes place in the human ovum, an inference which has been of late years fully justified by direct observation. In discussing this part of our subject, we shall, therefore, infer that the early embryonic changes occur in a similar order, and are of the same essential character in all mammalia, except, of course, with reference to the precise period at which they take place, which necessarily differs in various animals, according to the duration of pregnancy. For much that we know of the development of the mammalian ovum, we are indebted to the beautiful researches of Bischoff upon the ova of the dog, rabbit, guinea-pig, and deer.

Primitive Streak.—At a period varying from the twelfth to the sixteenth day, the dog's ovum assumes a more oval form. It is about three lines in length, and about a line and a half in its short diameter. Its external surface is as yet perfectly smooth, for none of the tufts or villosities of the chorion are developed. The central clear space (area pellucida or germinitiva) is seen to be surrounded by a darker circle, which eventually becomes the *vascular area*.

In the centre of the clear space a line is soon observed. This is the first trace of the embryo, *the primitive streak*, which appears in the form of a straight white line, or very shallow groove. It lies across the short axis of the ovum, and therefore occupies a position precisely similar to the embryo chick.

The primitive streak is formed in the serous or animal layer of the germinal membrane, beneath the *investing membrane* of Reichert. Bischoff has shown, that in the mammalian ovum the germinal membrane becomes divided into two laminæ, as in the

Fig. 276.



Portion of the germinal membrane of the bitch's ovum, showing the area pellucida and first traces of the embryo, after Bischoff. *a.* Germinal membrane; *b.* area vasculosa; *c.* area pellucida; *d.* laminæ dorsales; *e.* primitive trace. Magnified ten diameters.

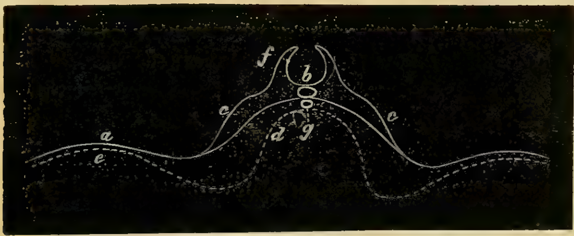
chick. The external lamina is the serous, or animal layer, and the internal one is the mucous or vegetative layer. The middle layer, or *membrane intermedia*, described by Reichert, has already been alluded to in page 582, but according to Bischoff is not to be detected in the mammalian ovum.

Formation of Dorsal and Ventral Laminæ.—In a short time the cephalic extremity becomes enlarged, and the entire embryo of a guitar-shape in its general outline. As soon as the primitive groove is formed, two oval folds are seen to rise up on each side of it from the serous laminæ (*d.* fig. 276). These are the *laminæ dorsales,* which gradually approximate; and the groove between them becomes converted into a canal which contains the central organs of the nervous system.

Reichert supposes that the laminæ dorsales actually take part in the formation of the central parts of the nervous system; but Bischoff considers that they represent the dorsal portion of the embryo, and that the nervous system is developed from their lower

and inner part only. About this time a few small square-shaped plates make their appearance in the central portion of each dorsal lamina. These plates are the first rudiments of the vertebræ. The soft *chorda dorsalis,* a structure which exists permanently in the lower cartilaginous fishes, appears subsequently between the rows

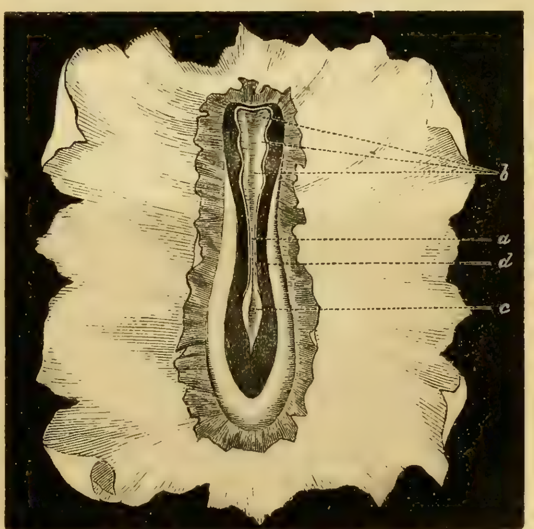
Fig. 277.



Plan shewing the mode of development of the dorsal and ventral laminæ. *a.* Serous or animal layer; *e.* mucous or vegetative layer; *b.* chorda dorsalis; *c.* ventral laminæ, arching downwards to enclose the intestines, the rudiment of which is shown at *d.*; *f.* dorsal laminæ arching over to convert the groove into a canal for the spinal cord; *g.* aorta.

of plates, but this is by no means so distinctly marked in the mammalian ovum as it is in the embryo frog or fish, while in the lowest cartilaginous fishes, as the myxine, the lamprey, and others, it is persistent. The two plates of opposite sides gradually approximate, and ultimately coalesce, including between them a portion of the chorda dorsalis, a temporary structure, which disappears entirely without being transformed into any more permanent texture.

Fig. 278.



Germinal membrane with rudiments of embryo of the dog. After Bischoff *a.* Primitive groove, not closed; *b.* the three dilatations corresponding to the three vesicles of the cerebrum; *c* space at lower part of groove or *sinus rhomboidalis.* The streak at the bottom of the groove is the chorda dorsalis.

The *laminæ viscerales,* or *ventral laminæ,* are also developed in the serous layer, and continuous with the laminæ dorsales. They

project downwards, and ultimately enclose the anterior portion of the embryo.

In the anterior dilated extremity of the embryo are developed three vesicles, from which the different parts of the brain are ultimately evolved.

Formation of the Amnion. — The upper layer of the serous lamina becomes raised in the form of a convex ridge, which extends entirely round the circumference of the embryo. This ridge, consisting of course of two layers of serous lamina, rises up gradually, and the two portions from opposite sides approximate above the dorsal surface of the embryo. The parts of the fold corresponding to the anterior and posterior extremities of the embryo grow faster than other portions, and soon two considerable reduplications are formed. These are called the *cephalic* and *caudal involucra.* The embryo is gradually enclosed by these two layers, which meet over its dorsal surface, and at last coalesce. Thus is formed the *amnion;* and the interval between the inner layer and the embryo is the *amniotic cavity,* which contains a fluid, the *liquor amnii.* The two layers, after some time, become united into one, except at the points where they are separated by the allantois and umbilical vesicle, forming the single amniotic membrane, which lies within the chorion. The outer layer, however, is separated from the inner surface of the chorion by a quantity of viscid albuminous matter which is subsequently absorbed.

The mode of formation of the amnion in mammalian ova is therefore precisely similar to that of the chick, according to

Fig. 279. *Fig.* 280.

Plans showing manner of formation of amnion, allantois, and umbilical vesicle. *a.* Chorion with villi, most abundant in that part beneath which the allantois is seen in figure 280: this portion ultimately becomes the placenta. *b.* Space between the two layers of the amnion. *c.* Amniotic cavity. *d.* Situation of intestine, showing its connexion with the umbilical vesicle. *e.* Umbilical vesicle. *f.* Situation of heart and vessels. *g.* Allantois.

Von Baer. Reichert, however, considers that it is formed in a somewhat different manner to that above described.*

In mammalia, the formation of the amnion occurs at a very early period, usually within twenty-four hours after the first appearance of the primitive trace.

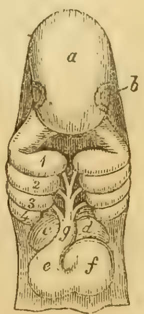
About the twentieth day the ovum is about ten, and the embryo is between three and four lines in length. The villi of the chorion are beginning to make their appearance, and gradually extend themselves round the ovum. That portion, however, which is immediately beneath the embryo is the last part of the surface upon which villi appear, while the two ends of the ovum always remain smooth and uncovered with villi.

By this time, with the exception of their posterior portion, the laminæ dorsales have coalesced, and the vertebral plates have increased in number. The position of the eye and ear can be determined, and the anterior surface of the body is being gradually closed in by the convergence of the *ventral laminæ* which spring from the under part of the dorsal laminæ. At length the body of the embryo appears entirely pinched off as it were, and is only connected with the yolk sac or umbilical vesicle by a narrow constricted portion, *the omphalo-enteric duct.*

Branchial Fissures and Arches.—At this period, three branchial fissures and three visceral arches may be detected.

The term *branchial* arch is a bad one, since it conveys the idea that, at a certain period, branchiæ are developed in the higher vertebrata, which is not the case. The only structures representing the branchial vessels of fishes are branches which unite to form the descending aorta. In fishes, the arches become permanent, and are surmounted by branchial laminæ. They are five in number; at a very early period there are six, but *one* is not further developed. In the amphibia a similar process takes place, but here the branchiæ waste away when the animal assumes its adult form. Usually only two, very rarely four, arches remain in reptiles; and in birds, mammalia, and man, only one is persistent.

Fig. 281.



Visceral or branchial arches of an embryo dog, after Bischoff. *a.* brain; *b.* eyes; *c. d.* right and left auricles; *e. f.* right and left ventricles; *g.* aorta dividing into aortic arches. 1, 2, 3, 4, corresponding visceral or branchial arches.

Heart and large Arteries.—About this time also the heart and large vessels are formed. The heart appears first in the form of a narrow elongated

* Müller's Physiology, translated by Dr. Baly, p. 1552.

tube, which is a little twisted, and gradually becomes completely bent upon itself. The development of the heart may be watched in the chick from the beginning of the second day of incubation. It appears between the mucous and serous laminæ in the form of a sac, terminating in two or three branches, the future venous trunks. At this early period even rhythmical motions may be observed, but the fluid in its interior is at this time nearly colourless. The large vascular trunk immediately after its origin from the ventricle divides into four vascular arches, which unite again to form the aorta. This vessel, as it passes down close to the spine, again divides, and gives off transverse branches; some of which, the arteriæ omphalo-mesentericæ, lying upon the duct of the same name, are conducted to the yolk-membrane, upon the surface of which they are spread out. These vessels absorb the nutrient constituents of the yolk, and carry them to the system of the fœtus. With their corresponding veins they form a network over the umbilical vesicle. Their arrangement will be more fully described in chapter xliii., on the development of the membranes of the fœtus.

Allantois.—The allantois is first observed as a little solid eminence composed of cells upon the anterior surface of the caudal extremity of the embryo (figs. 279, 280 *g.*). A cavity is soon formed, which is continuous at one period with the lower part of the intestine.

The allantois grows very rapidly, and in ruminants soon surrounds the entire fœtus, its outer surface being in close contact with the chorion; but in rodent animals, and in man, its chief office is probably that of conducting the vessels of the fœtus to the chorion.

Development of the Human Embryo.

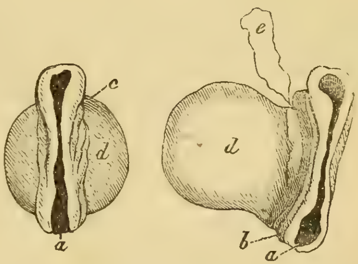
It was formerly supposed that man, in his development, passed through various successive stages, each of which was said to have its permanent representative among the lower animals; but a doctrine so obviously untrue has long since ceased to have any supporters. Von Baer showed the fallacy of such a statement; but at the same time proved that up to a certain period of development, the changes occurring in the human embryo were precisely similar to those which take place in the development of all other vertebrate animals; that, for instance, up to a certain period of its existence, we should be unable to distinguish the embryo of man, or one of the higher vertebrata, from that of a

reptile or a fish. All seem to be developed upon one general plan. The organs are evolved in the same order, and the organic functions in the manner of their performance are precisely analogous. After this point has been reached, however, the distinctive characters are well marked, and then it is very easy to say whether the embryo is to assume permanently the condition of a fish, reptile, bird, or mammal.

One of the youngest human ova which has been examined, is described by Mr. Wharton Jones, and was aborted in the third or fourth week after impregnation. It was about the size of a pea, and was probably detached at a somewhat earlier period. Villi were seen on one side only of the chorion. At one end of the ovum, lying in the midst of a gelatinous material, was the germinal vesicle, but the embryo was not yet visible upon it.

Dr. Allen Thomson has examined two human ova at a somewhat later period. One was a quarter of an inch, and the other half an inch, in diameter. The embryo was about one line in length (Fig. 282). It lay nearly flat upon the yolk-sac, no constriction being as yet formed. The dorsal laminæ were distinct, and had not yet united together. There was neither allantois nor amnion. This ovum was examined about fifteen days after conception.

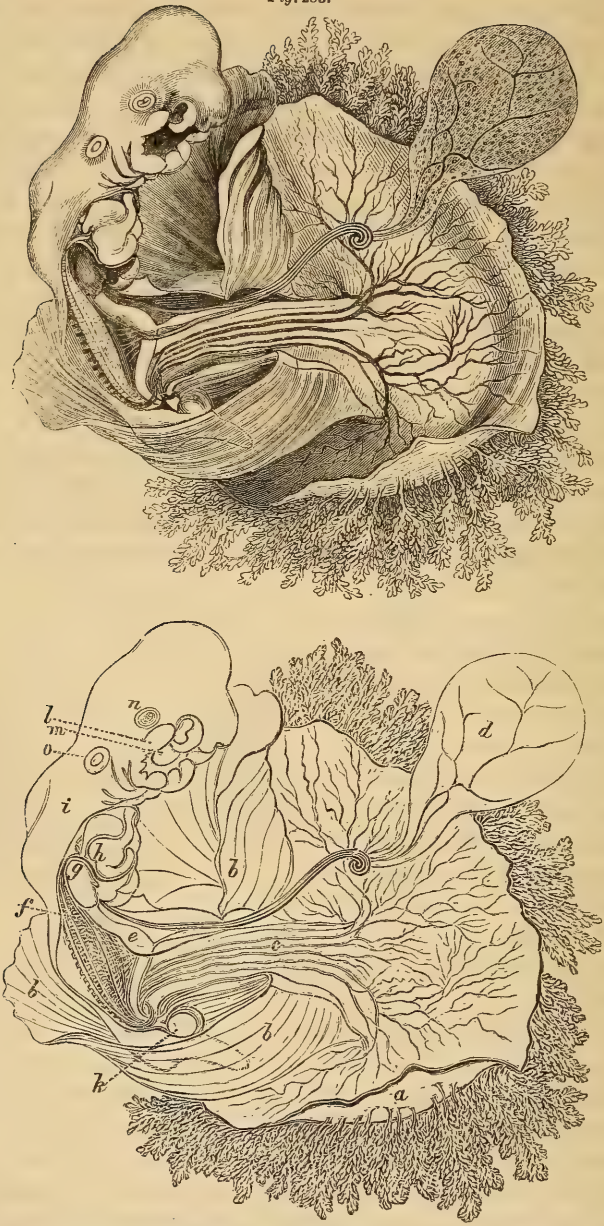
Fig. 282.



A Human ovum described and figured by Dr. Allen Thomson, about fifteen days after conception, magnified ten diameters. *a.* The open vertebral canal, bounded by the laminæ dorsales. *b.* Folds of the intestinal groove. *c.* Position of the heart. *d* Yolk sac. *e.* A piece of membrane perhaps connected with the formation of the Chorion.

MM. Pockels and Coste have had an opportunity of examining an ovum about this period, in which the umbilical vesicle and allantois were seen very distinctly. The embryo lay in the amniotic fluid; but the allantois had not yet become connected with the inner surface of the chorion. In another embryo described by Dr. Allen Thomson, about five or six weeks after conception, the allantois was attached to the chorion, and there existed an umbilical cord, which was not yet enclosed in its sheath formed by the amnion. It was the eighth of an inch in length. The heart projected in the form of a looped vessel from the anterior aspect of the body. The intestine was straight and opened into the yolk-sac, and the opening of the anus was not yet formed. The umbilical vesicle was becoming narrower near the embryo. Two branchial

Fig. 283.



Human fœtus between the twenty-fifth and twenty-eighth days, to shew the relative position of the several organs. *a.* Chorion with tufts developed over the greater part of its surface. *b.* Amnion; between the situation of the two *b*'s the amnion forms a sheath which invests the structures which compose the umbilical cord. *c.* Position of Allantois with the vessels upon it which ramify in that part of the chorion where the placenta is developed. *d.* Umbilical vesicle with its narrow pedicle and trunks of omphalo-mesenteric vessels which spread out upon its surface. *e.* The point at which it opens into the intestine. *f.* Corpora Wolffiana. *g.* Liver. *h.* Heart. *i.* Rudiments of anterior; and *k* rudimentary posterior extremities. *l.* Branchial fissures and visceral arches. *m.* Cavities of nose and mouth not yet separated. *n.* Rudimentary eye. *o.* Rudiments of ear. After Coste.

fissures were present. Wagner and Müller have examined ova a little further advanced. The embryo examined by the latter observer was two and a half lines in length, and the amnion was seen closely applied to it. There were three pair of branchial fissures and arches. The age of this embryo may be stated with tolerable certainty to be about twenty-five days.

Several human ova have been subjected to careful examination by different observers, between three and four weeks old, which may be considered to be in a normal state, and not modified by the occurrence of any morbid change. At this time, the ovum is about seven lines in length, and the embryo not more than two. It is surrounded by an amnion which adheres to it pretty closely. The chorion is already covered with small villi. Between the chorion and amnion is a considerable quantity of a viscid albuminous material. The embryo is curved. The anterior cerebral vesicles are well marked, and immediately behind them are the very large corpora quadrigemina. The positions of the opthalmic and auditory vesicles are indicated. Three or four visceral arches are seen with the branchial fissures between them. The heart is not yet fully formed, and projects from the anterior surface of the body as a bent tube. The anterior and posterior extremities exist in the form of curved flattish appendages. The abdomen is completely open, and the amnion is reflected over the anterior and posterior extremity of the embryo to form the cephalic and caudal involucra.

The heart is large, and consists of a simple auricle and ventricle. Behind the heart is seen the liver, beneath which is situated the intestine attached by its mesentery. The umbilical vesicle is as large as the embryo, and it is connected with the intestine by a long pedicle, the *ductus omphalo-entericus.* The vesicle itself is found lying between the chorion and amnion (Figs. 280, 294). The duct, with the vessels which accompany it, and the allantois, constitute the umbilical cord, enveloped by the amnion, which membrane forms a tube enclosing these structures.

The *allantois* is seen as a large and well-defined vesicle, which extends to the inner surface of the chorion, to which it is attached. On each side of the mesentery, close to the spine, are situated the large *Wolffian* bodies.

About the fourth week, there are three branchial fissures and arches behind the lower jaw. The divisions of the vertebræ are very distinctly marked, and in consequence of the curvature of the embryo, the coccyx and forehead are brought very close together.

Up to this period, the development of the human embryo is very similar to that of other vertebrate animals.

The umbilical vesicle, about four or five lines in diameter, diminishes considerably in size during the third month.

The viscid albuminous material between the chorion and amnion gradually becomes absorbed, in consequence of which these two membranes approach each other, and almost come into contact, but they still remain separated by a thin membrane, the *tunica media* of Bischoff.

The villi of the chorion increase very much in that portion of its surface situated over the allantois, where the placenta is to be formed. They are not absorbed from other parts, but the interspaces between them gradually become much greater; and as the ovum increases in size, the tufts appear to be almost limited to the position of the placenta, although, with care, they may be seen in other parts of the surface.

The cord gradually increases in length, and the quantity of liquor amnii, in which the ovum floats, becomes greater.

Ossification commences towards the end of the second month, when the fœtus is about an inch in length. The septum of the heart begins to be formed, and the aortic arches diminish in number to two, which unite behind to form the descending aorta. One of these arches becomes the pulmonary artery. The development of the kidneys, ovaries, testes, and external generative organs commences. The bladder is formed somewhat later by the pinching off of a portion of the *urachus*, a narrow tube, which is all that remains of the allantois. The cavities of the mouth and nose are not yet separate; but the divisions between the fingers and toes are commencing to be marked.

During the third month, the embryo increases from one inch to about two and a half or three inches in length. In the fourth, it increases another inch; but during the fifth month it grows so rapidly as to attain the length of twelve inches. Fat is formed about this time, and the nails are developed. The first movements of the fœtus felt by the mother, and termed *quickening*, usually take place between the fourth and fifth month. The whole surface is covered with *lanugo* or soft down. The very slow growth of the fœtus during the time when the organs are being evolved, and it is assuming its distinctive characters, contrasts very remarkably with its rapid increase in size as soon as the various organs have attained a definite form. The process of *evolution* is a complicated one, and obviously requires much time for the occurrence of the necessary transitional changes. The process of *growth* is a simple one, and consists merely of the appropriation of new material

by structures already formed. The further development of the different textures gradually takes place, and the various organs assume their permanent character, until about the seventh month the fœtus has attained a length of sixteen inches or more, and under favourable circumstances, its life may be preserved if it be born at this early period. The testicles descend about the eighth month.

By the end of the ninth month the fœtus has attained the length of eighteen or twenty inches. The head is covered with hair, and the skin becomes invested with a soft pultaceous substance, the *vernix caseosa,* which consists of cells of epidermis, with a considerable quantity of oily material. The *membrana pupillaris* is absorbed. During the latter months of pregnancy, the child lies in utero, with its head downwards, the position in which birth takes place.

The student is referred, for further information upon the subjects treated of in the present chapter, to the works enumerated at the end of chapter xl., and to the following:—Reichert's Observations on the Development of the Chick, in Müller's Physiology; translated by Dr. Baly. Bischoff's Monographs on the Development of the Dog and Guinea-pig. De Graaf, Opera Omnia. Von Baer's Entwickelungs-geschichte. Dr. Thomson, in the Edinburgh Med. and Surg. Journal, No. 140. Wagner, Icones Physiol. Article Ovum, in the Cyclopædia of Anatomy and Physiology by Dr. Allen Thomson.

CHAPTER XLII.

ON THE DEVELOPMENT OF THE DIFFERENT ORGANS.—DEVELOPMENT OF THE SPINAL COLUMN.— OF THE FACE AND VISCERAL ARCHES.— DEVELOPMENT OF THE NERVOUS SYSTEM.—OF ORGANS OF VISION AND HEARING.—DEVELOPMENT OF THE HEART AND AORTIC ARCHES.—OF THE ANTERIOR VENOUS TRUNKS.—OF THE LUNGS. —OF THE THYROID.—DEVELOPMENT OF THE ALIMENTARY CANAL. —OF THE LIVER AND PANCREAS.—OF THE SPLEEN.—DEVELOPMENT OF THE WOLFFIAN BODIES AND KIDNEYS.—OF THE SUPRA-RENAL CAPSULES.—OF THE ORGANS OF GENERATION.

In the present chapter we have to consider the mode of development of the most important organs of the body; but we do not propose to enter further into the process of development of the separate tissues, as this part of the subject has been already treated of in the preceding chapters upon the anatomy of the different organs.

Development of the Spinal Column.—In man and the higher vertebrata, the spinal column is composed of a number of distinct and separate segments, which are connected together by the intervention of a fibrous material. This gives to the whole column a considerable amount of mobility. In the lower fishes, however, no such division exists; and in the place of numerous vertebræ we have a continuous mass of a soft consistence running through the whole length of the animal, and known as the *Chorda Dorsalis.* The material of which this is composed is the simplest form of cartilage, consisting entirely of a number of large cells, without the interposition of any matrix or intercellular material between them. In the embryonic condition of all vertebrate animals, we meet with a chorda dorsalis entirely composed of cells, and possessing similar characters to the permanent chorda dorsalis of the cartilaginous fishes. It is seen as a faint streak at the bottom of the primitive groove. Above it, the central organs of the nervous

system are formed; and immediately beneath it, is the great artery of the body, with the viscera. At the anterior and posterior extremities of the embryo, the chorda dorsalis tapers to a point. In its earliest condition, it is composed of a perfectly clear gelatinous material, in the anterior extremity of which cells soon make their appearance, and increase in number until the whole becomes cellular. It is surrounded by a delicately fibrous sheath; external to which the blastema, which gives rise to the development of ossifying cartilage, is deposited. In this situation, after a time, cartilaginous rings make their appearance, and merge by insensible gradations into the fibrous sheath. The fibrous structure gradually disappears, and in its place cartilage is formed, while at the same time the substance of the chorda is removed, to give place to the developing cartilage. The cells of the cord, however, are not *transformed* into cartilage cells. Eventually only a portion of the cellular substance remains between the bodies of the vertebræ. At a much later period, cartilaginous arches are formed in the inner part of the dorsal laminæ, which become converted into the *vertebral arches*. The outer portion of the laminæ dorsales becomes converted into muscular tissues and integuments.

The *cranium* is originally formed from an extension forwards of the chorda dorsalis, and its development occurs at a much earlier period than the bones of the face. In the lamprey and the sturgeon, the connection between the chorda and the cerebral cartilage is permanent. In mammalia, those portions analogous to the bodies of vertebræ appear in the basis cranii; and prolonged from these, above, are portions corresponding to the *neural arch* of the *typical vertebra;* and below, parts belonging to the *hæmal arch.*

The body of the *epencephalic* or *occipital vertebra* is represented by a distinct point of ossification, for the basilar process of the occipital bone; its *neural arch* by the expanded portion of the bone itself; its *hæmal arch* by the *scapulæ, bones of arm, fore-arm,* and *hand,* and the *coracoid processes of the scapula* (*coracoid bones* of oviparous vertebrata).

The body of the *mesencephalic* or *parietal vertebra* is seen in the *basi-sphenoid*, or body of the sphenoid bone; its *neural arch* is formed by the *mastoid portions* of the *temporal bones*, *the great wings* of the *sphenoid* and the *parietal bones;* its *hæmal arch* by the *styloid process* of the *temporal*, and by the *body* and *greater* and *lesser cornua* of the *hyoid bones.*

The *prosencephalic* or *frontal vertebra* has its body represented by the anterior or *spheno-orbital portion* of the *sphenoid;* its *neural arch*

by the *external angular processes* of the *frontal*, the *small wings* of the *sphenoid*, and the *frontal bone;* its *hæmal arch* by the *tympanic portion* of the *temporal bone*, and by the *articular and dental portion* of the *inferior maxilla.*

The body of the *rhinencephalic* or *nasal vertebra* is represented by the *vomer;* its *neural arch* by the *ossa plana* of the *ethmoid*, and by the *nasal bones;* its *hæmal arch,* by the *palatine, pterygoid,* and *malar bones*, by the *squamous* and *zygomatic* portions of the *temporal bones*, and by the *superior maxillary* and *intermaxillary bones.*

In thus briefly describing the manner in which the cranial vertebræ are constructed, we feel great regret that our limited space will not permit us to enter more at length into the beautiful and well-known discoveries of Professor Owen in this department. We cannot too strongly recommend the reader to consult upon this important subject, Professor Owen's "Archetype Skeleton," and his "Homologies of the Vertebrate Skeleton."

Development of the Face and Visceral Arches.—The visceral cavity in the upper part of the embryo, at a very early stage of development, is bounded above by the cerebral capsule; and below, and at the sides, by the anterior visceral arch. Reichert has shown that this arch becomes bent upon itself, and from it are formed above the angle, the *superior,* and below the angle the *inferior, maxillary* apparatus.

The *superior maxilla* grows upwards, and unites with a prominence which is seen in the centre of the forehead, the *frontal process* of Von Baer — a space being left between the two superior maxillæ, which becomes the *nasal cavity.* Beneath this, the two bones are connected together by the partition which forms the palate, and which does not appear for some time.

In animals, besides the maxillary bones, there are a pair of narrow bones between them, extending from the interval between the lower portion of the nasal, and the ascending process of the superior maxilla. These are the *intermaxillary bones*, which exist in the human fœtus in a rudimentary condition. They appear to be formed partly from the nasal process of the forehead, and partly from a portion of blastema which is detached from the lower jaw, to which Reichert gives the name of *intermaxillary rudiment.* In man this bone is not developed; but in fishes and amphibia it contains teeth. The intermaxillary bones differ, therefore, in their origin, from the maxillæ, and are probably developed from centres independently of the latter. In the monstrosity familiar to us as *hare-lip*, the superior maxillæ and palate bones of opposite sides do not

meet, while the intermaxillary bones are united in the centre, and form a prominent tongue of bone, on either side of which is a deep fissure between the *intermaxillary* and corresponding *maxillary bones* of each side—thus is produced the deformity of *double hare-lip*. The cleft of the palate in these cases usually remains open, and in this way the malformation is increased. The fissure of the *lip* seems to arise from the alteration of the deeper parts; for as such a fissure exists at no period of embryonic life in the soft parts, it cannot, like the bony fissure above described, be dependent upon an arrest of development.

The *first visceral arch* gives rise to the *superior maxillary apparatus,* consisting of the *intermaxillary bones*, the *vomer*, the *maxillary* and *palate bones*, and the *pterygoid plates* of the sphenoid, the *lower jaw*, and the *malleus* and *incus.*

The *second visceral arch* gives origin to the *hyoid bone*, the *styloid process,* and its ligaments, and the *stapes* of the ear. In animals a great part of this hyoid apparatus becomes ossified.

From the *third visceral arch* arise the *posterior cornu* and *body* of the *hyoid bone.*

In the embryo of mammalian animals, the fourth arch is very indistinct.

Development of the Nervous System.—Reichert has shown that, in their earliest condition, the central organs of the nervous system are composed of two laminæ united in the middle line, so as to form a central groove. This groove soon becomes converted into a canal, except in the position corresponding to the medulla oblongata. In front of this, certain vesicles appear, from which the several parts of the brain are subsequently developed.

These vesicles have been named *Prosencephalon*, *Deutencephalon*, *Mesencephalon*, and *Epencephalon,* by Professor Owen. Of these vesicles, the latter, which corresponds to the cerebellum, is at this early period the largest of the four. The *mesencephalon,* or vesicle of the corpora quadrigemina, corresponds to the large optic lobes in fishes, reptiles, and birds, which in these classes are only two in number (corpora *bigemina*), and in the adult human brain is represented by the small corpora *quadrigemina* (anteriorly *nates,* posteriorly *testes*). In front of this vesicle is a small one, which is formed before any of the others, and for some time is the most anterior of all. This is the vesicle of the *third ventricle,* and contains the *optic thalami.* These points are all well seen in the fish's brain.

The *prosencephalon,* from which the *cerebral vesicles* are formed,

lies in front of this, and at first is extremely small; it bears a proportion to the rest of the encephalon not greater than that which the small, unimportant cerebral lobes of the adult fish bear to its entire cerebrum. The prosencephalon soon, however, increases in size, and becomes much larger than all the others.

Our friend, Professor Retzius, has shown that the three lobes of the hemispheres of the human brain, are developed at different periods; the anterior being formed during the second and third months, the middle lobes between the end of the third and beginning of the fifth month, and lastly, the posterior lobes are produced. The cerebellum was seen by Von Baer, in the chick, during the fourth day of incubation. It is formed by the meeting of the laminæ of the spinal cord anteriorly to the fourth ventricle; a short canal is, however, left, which passes towards the corpora quadrigemina or optic lobes, the future *iter a tertio ad quartum ventriculum.*

Bischoff has demonstrated that, at a very early period, nervous matter is formed along the inner surface of the lips of the primitive groove. These two masses of nervous matter gradually approximate, and thus a tube is produced, the walls consisting of nervous matter—while the central cavity, after contracting, becomes the canal of the spinal cord. The upper portion forms the thin dilatations before described; while at the opposite end is seen a lancet-shaped depression, the future cauda equina, or *sinus rhomboidalis* in birds.

Development of the Organs of Vision and Hearing.—According to Mr. Gray, the eye of the chick is first seen about the thirty-third hour of incubation, in the form of a protrusion from the anterior vesicle, which corresponds to the cerebral lobes, and may be called the *optic vesicle.* This view agrees with that of Baer; but it does not accord with the observations of Wagner or Huschke. The latter observer states, that the eye is developed from a protrusion of the vesicle of the third ventricle—from the *deutencephalic enlargement.* The retina is a vesicular body which communicates with the cavity of the brain through the hollow, tubular optic nerve. These points may be observed in the chick during the second day of incubation. Bischoff and Mr. Gray have been unable to confirm the statements of Huschke, with reference to the doubling-in of the retina to form two layers. The latter observes that the fibrous lamina and Jacob's membrane are not developed until after the cellular layer of the retina is formed.*

* Phil. Trans., 1850.

About the third day of incubation a fissure, which commences at the border of the lens, is seen in the eye of the chick, which Huschke regards as the consequence of inversion of the retina. In fishes, the cleft running from the centre, towards the anterior border of the retina, exists throughout life. In the turtle there is a fissure in the nerve but not in the retina.

Jacob's membrane is not developed before the thirteenth or fourteenth day of incubation. Mr. Gray describes it as forming at this period an exceedingly fine pale granular stratum upon the choroidal surface of the retina.

The circle of the *iris* is seen in the anterior part of the choroid at a very early period; but the pupil is occupied by a highly vascular membrane, the *membrana pupillaris.* This is not attached to the margin of the iris, but to its anterior surface, from which it derives its vessels; and it is probable that it is reflected over the whole anterior surface of the iris, and possibly lines the anterior chamber of the eye. From the margin of the iris, there extends backwards another vascular membrane, the *membrana capsulo-pupillaris,* which is united to the border of the capsule of the lens. This membrane forms a closed sac, the anterior part of which is united to the membrana pupillaris; while the posterior portion lines the anterior concave surface of the vitreous body. This is supplied with vessels by the capsular branch of the arteria centralis retinæ; and at the margin of the iris, the vessels of the membrana pupillaris, and those of the membrana capsulo-pupillaris, communicate with those of the iris.

The *eyelids* are first developed in the form of a ring, which extends over the surface of the eye; and afterwards the two portions which are to be developed into the lids become adherent to each other. They separate again, either before birth, as in the human subject—or after birth, as in the carnivora and some other classes.

Organ of Hearing.—The ear appears, at a very early period, upon the vesicular protrusion which ultimately becomes the auditory nerve. It communicates with the cavity of the fourth ventricle, and is situated above the second branchial cleft. The first rudiments of the auditory vesicle were seen by Mr. Gray about the fiftieth hour of incubation in the chick. Throughout the life of the cyclostomous fishes, the ear retains the condition which it presents at an early period of development in the mammalia. Valentin describes the labyrinth as appearing in the form of a separate body of a somewhat elongated form. The inner extremity forms a turn

and at this point a second vesicle makes its appearance, which becomes the *cochlea.*

The semicircular canals are developed by a contraction and folding-in of the walls of the vestibule. From Mr. Gray's careful observations, it appears that the labyrinth, about the twelfth or thirteenth day of development in the chick, has an appearance closely resembling the retina at the same time—a point of great interest. Huschke has shown that the Eustachian tube, the cavity of the tympanum, and the external meatus, are the remains of the first branchial cleft, which eventually becomes divided by the membrana tympani.

The *ossicles* of the ear are formed as follows:—The *malleus* and *incus,* according to Reichert, are produced from the first visceral arch, which also gives origin to the superior and inferior maxillæ. The *stapes* appears to be produced from the second visceral arch, which also gives rise to the hyoid bone and its suspensory apparatus. The ossification of these little ossicles commences in the fourth month of intra-uterine life.

The development of the mouth and nose have already been alluded to at page 598.

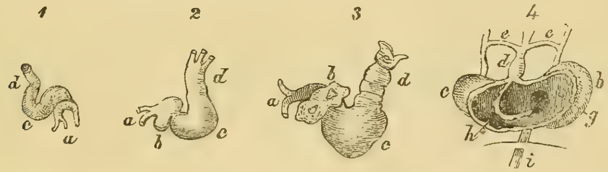
Development of the Heart and Aortic Arches.—The development of the heart is best studied in the chick. It appears towards the end of the second day of incubation, as a small hollow tube between the mucous and serous laminæ of the germinal membrane. About the thirty-sixth hour it has become a simple tube, much curved and twisted upon itself. Posteriorly, it terminates in two or three large venous trunks, which are insensibly lost on the germinal membrane; and anteriorly, it divides into two branches, which unite beneath the vertebral column to form the aorta. The trunk of the vessel again divides into two branches, which are lost on the vascular area. Early on the third day, the heart consists of three cavities — the *sinus venosus,* the *ventricle,* and the *bulbus aortæ;* the first soon becomes divided into the two auricles, and by the fourth day the ventricle assumes its usual form, and the formation of the septum, which divides its cavity into two portions, commences.

About the beginning of the third day, the aortic bulb divides into four pair of vascular arches. On the fourth day, the first pair disappears and is at length obliterated, and the second pair becomes smaller; but now is formed a fifth pair, which becomes larger on the fifth day, while the second entirely disappears; so that there are at this time only three pair, and these of nearly equal size.

About the sixth day, a considerable alteration takes place in the circulation. By this time, the allantois forms a vesicle of considerable size, upon the surface of which numerous vessels are spread out. These are derived from two branches resulting from the division of the aorta after it has given off the mesenteric artery. The allantois rapidly increases in size; and as the albumen diminishes in quantity, it becomes applied to the membrane of the egg-shell. Through the latter, and through the pores of the shell itself, the air passes to aërate the blood circulating in the vessels of the allantois, which may therefore be looked upon as the great respiratory surface of the chick previous to the formation of lungs.

About the sixth or seventh day, the heart acquires its characteristic form; its cavities have approximated more closely, and become conjoined; the division between the auricles and ventricles can be seen distinctly. The bulb of the aorta appears to arise from both ventricles, immediately over the septum; and its division into two canals is complete on the seventh day. The pericardium is formed. Only two vascular arches arise on the left side of the aorta, but on

Fig. 284.



1, 2, 3. Heart of chick at the 45th, 65th, and 85th hours of incubation. After Dr. Allen Thomson.— 4. Heart of a human embryo about the fifth week. After Von Baer.— *a.* Venous trunks. *b.* Auricle. *c.* Ventricle. *d.* Bulbus arteriosus. *e.* Two aortic arches, which unite posteriorly to form the *aorta*. *g.* Auriculo-ventricular opening. *h.* Septum arising from the lowest part of the cavity of the ventricle. *i.* Inferior vena cava.

the right there are three. The latter, and the two anterior arches, are the chief divisions of the aorta, and receive the blood transmitted from the left ventricle. On the seventh day, the two posterior arches receive blood only from the right ventricle, and become the pulmonary arteries. At present, however, all the arches terminate in the descending aorta.

At this period, the course of the blood is as follows:—From the system of the embryo it is carried by the *arteriæ vitellinæ*, or *omphalo-mesentericæ*, to the net-work of vessels of the vascular area, whence it passes to the sinus terminalis, which bounds the latter, and which, even on the fourth day, is found to be full of blood. The blood is returned to the heart by two anterior and two posterior venous trunks, arranged in pairs on each side of the median

line of the body. The anterior pair are the *jugular veins*, and the posterior pair are the *cardinal veins*, which carry back the blood from the Wolffian bodies and hinder parts of the embryo. Besides these trunks, however, there is a single one below, which receives the blood from the omphalo-mesenteric veins, and into this trunk the umbilical veins open subsequently. It becomes eventually converted into the *inferior vena cava.*

The pulsations of the heart commence before any cavity can be observed in the mass of embryonic cells of which it at first consists. Prevost and Lebert have observed the contractions before the development of any tissue distinctly muscular—a statement which we can confirm from observations upon the heart of the young field-snake (coluber natrix). Bischoff and Vogt also testify to the very early occurrence of pulsations.

In the human subject, about the fourth week, the septum between the ventricles commences to be formed. This is completed by the termination of the eighth week. The auricular septum, however, remains incomplete throughout fœtal life. The circulation in the fœtus, and the peculiarities of the fœtal heart, have been already described in page 348 of the present volume.

Aortic Arches.—In fishes, the vessel continuous with the bulbus arteriosus gives off on either side large branches, which are distributed to the gills; from these organs the blood is collected by small vessels, which ultimately re-unite to form a large trunk corresponding to the aorta, which lies immediately in front of the spine. In the early embryos of all vertebrate animals, similar branches, called *aortic arches,* may be seen; and these unite at the back of the visceral cavity, to form the descending aorta. They are visible in the chick about the fortieth hour, according to Dr. Allen Thomson.

In birds there are at first six aortic arches; but, as development proceeds, the number becomes less. In mammalia the arches soon diminish to three. One becomes the arch of the aorta, and the other two are the *ductus arteriosi* of the pulmonary artery, of which the right soon disappears, so that at length only two arches remain—one from the right, and the other from the left ventricle. The anterior part of the arch from the former becomes the trunk of the pulmonary artery; while the cavity of the posterior portion (*ductus arteriosus*), which leads into the aorta, gradually becomes obliterated, and soon after birth nothing remains of it but a fibrous cord, between the aorta and pulmonary artery, which marks its original position throughout life.

Anterior Venous Trunks.—At an early period of development of the human embryo, the veins entering the heart from the upper part of the body are symmetrical; and in many of the lower animals they preserve this arrangement throughout life. As the development of the human embryo advances the large venous trunk on the left side diminishes, and subsequently disappears entirely, leaving the right trunk only as a persistent vessel. In a valuable paper published in the Philosophical Transactions, Mr. J. Marshall shows, that the dilated portion of the coronary vein, the *coronary sinus*, is the persistent lower portion of the left anterior vein. It is interesting, that in animals which have a left superior cava, the great cardiac coronary vein opens into it. Even in the adult human heart there are certain structures which are obviously the remains of the upper portion of the left primitive venous trunk. These observations are very interesting, as they serve to explain certain unusual arrangements in the great anterior veins. Cases are recorded in which the two symmetrical trunks, usually only found at a very early period of development, remain persistent in the adult—an abnormal condition which receives explanation from the investigation of the nature of the early embryonic changes.

Development of the Lungs.—The lungs are first seen in the form of two small masses of cells, at the lower part of the œsophagus. These masses gradually increase in size, and a cavity is formed within. They coalesce at the upper part, which ultimately becomes the *trachea.* At this period of their development, the respiratory organs appear in the form of vesicles, appended to the lower part of the trachea.

Fig. 285.

Development of respiratory organs, showing origin of lungs from upper part of alimentary canal, after Rathke. A. Œsophagus of a chick on the fourth day of incubation. The rudiments of the trachea and lungs of the left side. 1. Inferior wall of the œsophagus; 2. superior wall; 3. rudimentary lung; 4. stomach. B. The same seen from below. C. Tongue and respiratory organs of the embryo of a horse 1. Tongue; 2. larynx; 3. trachea; 4. lungs seen from behind.

Reichert has shown that in the chick the lungs appear about the same time as the liver, and states, that although they seem to take their rise from the *membrana intermedia* (lying between the rudimentary nervous centres and the mucous membrane, p. 582), the upper portion of the visceral tube, according to his observations, is the real seat of their origin.

Thyroid Glands.—The first traces of the thyroid are observed in

the chick between the sixth and seventh days as a small spherical mass of blastema on each side of the root of the neck. In structure the thyroid resembles that of the spleen. Professor Goodsir describes the thymus, thyroid, and supra-renal capsules as arising from the membrana intermedia; but Mr. Gray, on the other hand, has pointed out that they are formed from separate and independent masses of blastema.

The development of the *thymus* gland, and its subservience to respiration, have been already considered in p. 521.

Development of the Alimentary Canal.—The alimentary canal is first seen in the form of an elongated straight tube, in which oil globules may be distinguished. According to Reichert's observations on the embryo of the frog, the walls of the intestine appear

Fig. 286.

Embryo dog, showing the junction of the umbilical vesicle, with the intestinal canal. *a.* Nostrils. *b.* Eyes. *c.* First visceral arch. *d.* Second visceral arch. *e, f.* Right and left auricular appendage. *g, h.* Right and left ventricle of the heart. *i.* Aorta. *k.* Liver, between the two lobes of which is represented the divided omphalo-mesenteric vein. *l.* Stomach. *m.* Intestine, communicating with the umbilical vesicle by the omphalo-mesenteric duct. *n.* Umbilical vesicle. *o.* Wolffian bodies. *p.* Allantois. *q.* The upper extremities. *r.* The lower extremities. After Bischoff.

to be formed originally from the most superficial cells of the yolk. The mucous membrane is developed from a thin layer of smaller cells of the yolk in the interior. Between the outer layer, which becomes converted into the muscular coat, and the inner layer, which constitutes the mucous membrane, a *glandular* layer is formed. From this tube the different parts are gradually evolved. The omphalo-mesenteric duct is connected with the lower part of the small intestine, just previous to its junction with the large intestine. The original connexion with the umbilical vesicle is sometimes marked by an elongated pouch, or diverticulum, persistent in the adult. The original yolk-cells, contained in the cavity of the intestine, slowly disappear. The length of the small intestine gradually increases, until it assumes its mature form.

The stomach, at an early period, is not wider than the rest of the canal, and its limits are not to be distinguished.

Originally, the tube of the intestine is completely closed, both at the mouth and anus. The membrane is gradually removed, and an opening formed. In cases of *imperforate anus* there is no opening, in which condition an operation is necessary, as soon as possible after birth.

Development of the Liver, and Pancreas.—The precise mode of origin of the liver in the embryo has not yet been ascertained with certainty. Some observers hold that this large gland is originally formed upon a diverticulum of the intestine, while others have concluded that it is developed from a distinct and separate mass of blastema. In the chick the first rudiment of this organ may be discerned between the fiftieth and sixtieth hour, and is described by Remak as consisting of two sets of cells — an external one, continuous with the external surface of the intestine, and an internal layer, composed of epithelium, and lining the sac, which ultimately becomes divided, so as to form the ducts. From the epithelial lamina the columns of liver cells are formed; these extend into the outer lamina, branch and anastomose, and include in the meshes thus produced, the cells of the outer surface, from which the vessels, nerves, and areolar tissue of the gland are developed.

Müller describes the liver, as formed on the fourth day of incubation, by a conical protrusion of the intestinal tube. The walls of the protrusion become very thick, and in their substance the ducts ramify.

According to Reichert, the liver and pancreas in the embryo

frog are developed from a portion of yolk, which becomes separated from the general mass at a very early period, and is penetrated by a prolongation, posteriorly, of the vessel continuous with the cavity of the heart. At first there is no appearance of a division in this mass of yolk substance, which becomes separated from the remainder before any trace of the alimentary canal has manifested itself. Subsequently, the two organs become more distinctly marked out. In the chick, according to the same observer, these organs are formed from a cellular growth upon the surface of the *membrana intermedia,* which is separated from the rest of this membrane. At first, the two lobes of the liver are of equal size, but, after a time, the right lobe preponderates, as it does in the adult.

Mr. Gray has figured the liver and pancreas of the chick. They seem to be developed from two separate protrusions of the intestinal tube, about the ninetieth hour of incubation. No vestige of the spleen is to be detected at this early period.

The following is Dr. Handfield Jones' account of the development of the liver in the chick. The parenchymatous portion is found to appear first; soon afterwards, an eminence, for which Dr. H. Jones proposes the name of *colliculus,* makes its appearance on the wall of that portion of the intestine which becomes the duodenum. From the latter tube pass two offsets to the liver; these, however, waste, but the *colliculus* remains. Subsequently, the cystic and hepatic ducts are developed close to the liver; they extend downwards, and open at the colliculus. In fishes and reptiles, the process of development is similar. Dr. H. Jones observes, that at one period the gall duct in tadpoles is lined by ciliated epithelium.

Reichert describes the formation of the columns of liver cells, and their increase in number; but he considers that the cells are not invested with basement membrane. This question has, however, been discussed in chapter xxxiii.

Spleen.—Mr. Gray has demonstrated that the spleen arises in a fold of the intestinal laminæ about the 114th hour of incubation in the chick; and it is probable that in the human subject its formation takes place during the third or fourth week. It is quite distinct from the pancreas from the earliest period of development.

The first traces of the splenic vein are seen about the thirteenth day of incubation; and the first blood discs appear in the organ about the eighth day. The Malpighian vesicles are not developed till about the twentieth or twenty-first day, when the period of in-

cubation is near its completion. It is probable that during fœtal life this organ plays no very important part, either in the development or destruction of blood corpuscles; and as the gall-bladder is found to contain yellowish-green bile, before the formation of the spleen, it is clear that this organ, at least in intra-uterine life, is not concerned in producing the colouring matter of that fluid—an office assigned to the spleen by Kölliker.

Wolffian Bodies.—The Wolffian Bodies are two small glands developed at a very early period, and situated upon each side of the spine, extending upwards for some distance. They lie in front of the kidneys and supra-renal capsules, figs. 283, 286.

Each Wolffian body is provided with an excretory duct, which opens into the cloaca or sinus urino-genitalis, whence its contents pass into the allantois.

These bodies are to be regarded in the light of temporary kidneys, and bear a similar relation to the permanent organs, that the temporary branchiæ of the tadpole bear to the lungs of the fully developed frog.

In osseous fishes, the corpora Wolffiana are permanent, and constitute the kidneys of this class of animals.

They are much elongated, and are composed of a number of transverse cœcal tubes arranged parallel to each other. At first they completely conceal the kidneys, but soon diminish in size, and are at length placed below those organs, which at the same are gradually assuming importance.

The Wolffian bodies are not eventually transformed into the epididymis, as some have held, or, indeed, into any other organ; but they disappear completely. The ducts of these glands, however, take part in the formation of the Fallopian tube in the female, and of the vas deferens in the male; and the last traces of the temporary corpora Wolffiana are found to have some relation to the generative organs. Their remains constitute the *parovarium* in the female (p. 554).

From the lower part of the excretory tube, in those animals whose uterus is bifid, its cornua are developed. In the human subject, although at a very early period there are two cornua, these soon coalesce with the central part of the organ which is being developed at the same time, and at last all traces of them are lost.

The corpora Wolffiana disappear at a much earlier period of development in the human fœtus, than in the lower mammalia; but Müller has figured traces of them in an embryo about 3½

inches in length. Each body was composed of numerous transverse cœca, passing from the Fallopian tube towards the corresponding ovary.

The *kidneys* are developed independently of the Wolffian bodies, and are situated on the inner side of the ducts of these temporary organs. As the latter gradually diminish in size, the development of the former advances.

Supra-renal Capsules.—The investigations of Mr. Gray upon the development of the supra-renal capsules in the chick, have proved that these bodies are not to be recognised before the end of the 7th day, when an ill-defined granular mass, of a reddish color, makes its appearance between the aorta and upper and inner sides of the Wolffian bodies. It seems to have no connexion with the thyroid or thymus, as Professor Goodsir described. Its minute structure resembled that of the spleen about the fifth day of incubation. By the 8th day, vesicles could be distinguished, and by the fourteenth day were found to contain oil globules, but no nuclei could be detected in their interior. The capsules were of large size, and of a yellow color by the 18th day, and now the division into *cortical* and *medullary* portions was quite distinct. The supra-renal capsules are developed from two separate masses of blastema, situated between the aorta and upper and inner extremities of the Wolffian bodies. They have no connexion with the latter, or with each other, and although in their minute structure they resemble the spleen, they arrive at their maximum of development before that organ.

Organs of Generation.—The sexual organs are developed at a later period than other glands. They are formed from masses of blastema situated upon the inner side of the upper and free part of the ducts of the Wolffian bodies. The ovaries and testicles are developed independently of the Wolffian bodies. At an early period of development the glands in both sexes have very similar characters, and it is not possible to say whether the organ is ultimately to become converted into a testicle, or whether it is to retain its primitive characters, which agree with those of the ovary. According to the observations of Valentin, the ovary of mammalian animals is developed in the form of tubes, in which the Graafian follicles are produced.

The *excretory ducts* in the lowest vertebrata are two in number, and open into the cloaca, an arrangement which is persistent in many fishes, but in the higher classes they are united, and form a single canal, the arrangement of which has been carefully investi-

gated by Müller. From this canal, in the male, is formed the *Weberian organ*, or *uterus masculinus,* while in the female it gives origin to the *uterus* and *vagina.*

The upper part of the excretory duct of the Wolffian bodies in the male becomes much modified in character, and is ultimately converted into the *epididymis,* whilst the lower portion becomes the *vas deferens.*

The lower part of the urino-genital canal, which becomes converted into the external organs of generation, for some time presents a cleft or fissure on its inferior surface, which in male reptiles and birds remains open throughout life, but in mammalia becomes converted into a canal, which extends to the tip of the *penis* in the male, or along the under surface of the *clitoris* in the female. Sometimes, however, a portion remains open, and the wall of the urethra is deficient in its anterior part below, when the congenital deformity known as *hypospadias* results. The folds of skin which bound the furrow ultimately become converted into the scrotum of the male, or labia of the female. The testicles descend into the cavity of the scrotum about the eighth month, but not unfrequently are retained within the abdominal cavity.

The authors would refer particularly to the following works with reference to the subjects discussed in the present chapter:—Müller's Physiology; Rathke, Beitrage zur Geschichte der Thierwelt; Valentin, Entwickelungs-Geschichte; Dr. Handfield Jones on the Structure and Development of the Liver, Phil. Trans, 1849; Victor Carus' System der Thierischen Morphologie; Reichert, das Entwickelungsleben im Wirbelthier-Reich; Mr. Marshall's paper On the development of the great anterior veins in man and mammalia, Phil. Trans., 1850; Mr. Gray's papers on the development of the ductless glands in the chick, Phil. Trans., 1852; and his paper on the development of the retina and optic nerve, and of the membranous labyrinth and auditory nerve, Phil. Trans., 1850.

CHAPTER XLIII.

OF THE MEMBRANES OF THE FŒTUS.—OF THE STRUCTURE OF THE CHORION.—OF THE AMNION.—LIQUOR AMNII.—OF THE UMBILICAL VESICLE.—OF THE ALLANTOIS.—ALLANTOIC FLUID.—UMBILICAL CORD.—BIRTH.

Formation of the Placenta.—The early development of the chorion has been described in a former page. At first, the villi are composed entirely of cells, invested on their external surface with a very delicate structureless membrane; but after the vessels, conducted by the allantois, have reached its inner surface, vascular loops are prolonged into them. Bischoff considers that in the human ovum, and in that of the bitch, which are destitute of an albuminous covering, the tufts are formed directly from the zona pellucida alone.

In two orders of mammalia, the *marsupialia* and the *monotremata*, there is no connection between the vascular system of the mother and that of the fœtus, which is nourished from a very early period with milk.

The relation between the blood of the fœtus and that of the mother is nearly the same in all placental mammalia. The wall of the maternal vessels,—a layer composed of cells from the modified mucous membrane of the uterus,—and another cellular layer belonging to the fœtal tuft, always separate them; but in the greater number of mammalia, the fœtal tufts come into relation with the *capillary vessels* of the mother; while in *man* they are in contact with the walls of a *large cavity* containing blood.

The mode of arrangement of the tufts, or, in other words, the form which the placenta assumes, is very different in the various mammalia. Sometimes the whole chorion is covered with villi, as in the *pachydermata* (hog, elephant, etc.); sometimes these form little collections or cotyledons, as in the greater number of *ruminants* (sheep, ox, goat, etc.); sometimes they form a band encircling the central portion of the chorion, as in the *carnivora*; and in some instances they are confined to one single part, forming a single placenta, as in the *rodentia*, and also in the *human subject* (vide figs. 280, 292).

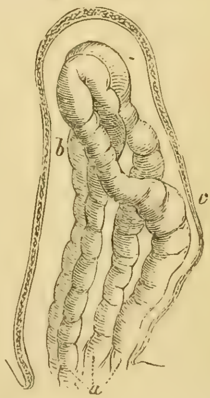
The beautiful branched and highly complicated conical *fœtal villi* of the ruminant dip into deep recesses in the *maternal cotyledons*, upon the walls of

which the maternal capillary vessels are spread out; while the vascular loops of the human fœtus, as was shown by Professor Weber, dip into the dilated vessels of the mother, which become large venous sinuses, and are thus completely bathed on all sides by the mother's blood.

The villi increase very much in number and complexity in that part of the chorion which is to become the placenta; while on other parts of the surface they retain the same characters as at a very early stage. Each villus contains a vascular loop, which is directly continuous with the umbilical vessels of the fœtus; and the whole of the blood of the fœtus is made to pass through the vessels in the tufts by the forces of the fœtal circulation. The cells of which the villi were entirely composed, at a very early period diminish in number; but still several remain towards the apex.

During this time, the soft membrana decidua has been increasing in thickness and vascularity. Its capillary vessels become enormously increased in diameter, and ultimately form small pouches or sinuses containing blood. The fœtal tufts come into close relation with the walls of these sinuses, but are still separated by a thin layer of the cellular decidua, and project into their interior, being of course invested with the wall of the sinus, just as the viscera are covered with peritoneum. Such is the relation of the blood-vessels of the fœtal placenta to those of the mother, according to the observations of Dr. J. Reid, Weber, and Goodsir. The structures, therefore, which intervene between the blood of the fœtus and that of the mother, are the following: the walls of the fœtal capillaries; the cells at the extremity of the fœtal tufts; the delicate investing membrane covering these; a thin stratum of fluid separating the maternal and fœtal portions of the placenta, and containing not only the materials for absorption but any substances to be removed from the fœtal blood; the cells of the membrana decidua; and, lastly, the wall of the venous sinus, into which the fœtal tuft projects.

Fig. 287.



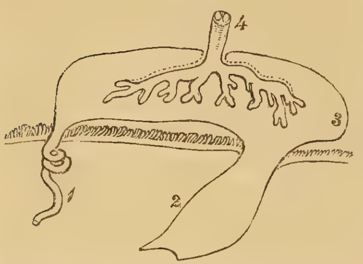
Extremity of a villus, showing capillary vessels. After Weber.

The cells upon the surface of the villus form little groups, and appear to radiate, as it were, from the centre of each collection. This central point, Professor Goodsir regards in the light of a *germinal spot or nutritive centre*, which

supplies successive generations of cells as the old ones are gradually removed.

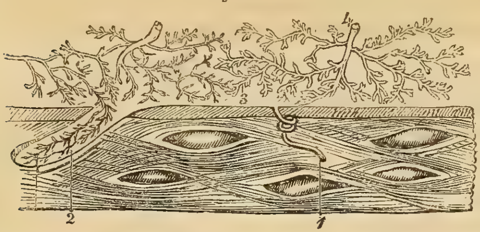
The wall of the venous sinus of the mother, reflected from tuft to tuft, forms numerous tubular processes, passing in various directions amongst them; thus connecting the several tufts with each other, and forming a sort of supporting framework for the entire organ. The tubular prolongations, of course, contain cells of the decidua in their interior, and by their outer surface are continuous with the lining membrane of the venous sinuses of the mother. Dr. J. Reid has shown that the fœtal tufts often dip quite into the uterine sinuses.

Fig. 288.



Relation between the fœtal and maternal vessels; after Dr. Reid. Fœtal tuft dipping into dilated venous sinus. 1. Curling artery of uterus. 2. Uterine vein. 3. Sinus. 4. Vessels of fœtal tuft, composed of a small branch of artery and vein.

Fig. 289.



Uterine sinuses and fœtal tufts; after Dr. Reid.—1. Curling artery of the uterus. 2. Uterine sinus, into which a tuft is prolonged. 3. Fœtal tuft. 4. Fœtal vessels branching.

Weber has made some beautiful injections of the fœtal tufts, which demonstrate very satisfactorily the highly tortuous nature of the capillaries, and show that the convoluted capillary vessel may make many turns from one fœtal loop into another, before it opens into one of the branches of the umbilical vein. Dr. Reid describes the blood brought by the curling arteries of the uterus as being poured "into a large *sac* formed by the inner coat of the vascular system of the mother," from which the blood is carried back by the veins. The researches of Dr. J. Reid agree with those of Weber; but Eschricht holds, that in man the arrangement is essentially the same as in animals; and that the capillaries of the placenta of the human fœtus are brought into relation with the capillaries only of the mother. In many animals, the maternal and fœtal portions of the placenta can be very readily separated from each other; but in man this cannot be done without tearing the vessels.

The formation of the placenta commences in the human subject

towards the end of the second month; and by the third it assumes its ordinary character. As the uterine vessels become enlarged,

Fig. 290.

Villi of the fœtal portion of a placenta; after E. H. Weber.—1. Artery. 2. Vein. Magnified 100 diameters.

the rush of blood through them is accompanied with a well-known murmur, termed the *placental bruit,* which is usually detected about the third month. It is one of the most important signs of pregnancy, and is not liable to be mistaken for the sounds of the fœtal heart, because it is exactly synchronous with the mother's pulse, and its situation does not vary.

Towards the termination of the period of pregnancy, the placenta becomes hard, and a curious change takes place in its capillary vessels, which has only been carefully investigated within the last few years. The alteration consists in the appearance of a number of oil-globules in the coats of the vessels—in fact, in the occurrence of *fatty degeneration* of the fœtal tufts. In a former page, we described a similar change taking place in muscular fibre-cells of the uterus, when the period of their activity was passed, and the organ was gradually returning to its former volume. The change alluded to has been looked upon by many pathologists as of a morbid nature, and has been brought forward as one of the causes of abortion; but the observations of our friend, Dr. Druitt,* and others, show that fatty degeneration of the vessels occurs in

* Medico-Chir. Trans., vol. xxxvi.

the great majority of placentæ which are subjected to examination, although in some it is much more advanced than it is in others. It occurs first in those tufts situated at the circumference of the placenta, in which part the functions of the organ cease first. In numerous instances, also, small masses of earthy phosphates are found in the fœtal tufts. Although fatty degeneration is doubtless to be regarded, in many instances, as a morbid alteration, we must at the same time bear in mind, that it does occur as a normal process, and is one of the changes which ensues in tissues prior to their absorption, after the period of their functional activity is brought to a close. It seems to be one of the first of a series of changes which ends in the removal of the tissue, or in the complete disappearance of its ordinary characters.

From what we have already said with reference to the structure of the human decidua and placenta, it follows, that both are separated at birth, and must be renewed at each successive pregnancy. Both the uterine and fœtal portions of the placenta are removed, and of course a considerable lesion takes place at the time. The great uterine veins are torn across, and the violent contraction of the uterus alone prevents the death of the mother from hæmorrhage at each period of parturition. Should the uterus, from any cause, fail to contract, the death of the mother from hæmorrhage is inevitable, as the experience of almost every practitioner but too clearly proves. Such a result, however, would not happen in the ruminants, and in some other animals, where the fœtal tufts are readily withdrawn from the maternal sheaths, which merely contract after parturition, and become much smaller, but suffer no lesion whatever.

Amnion.—The early stages of the development of the amnion have been already fully described (page 584). It is formed upon the same plan in all classes of animals, as it is in the human subject, as the later researches of Bischoff have conclusively shown. The human ovum, at an early period of development, is seen to be closely invested with the amnion; which membrane, originally consisting of two layers, is separated from the chorion by a considerable space, which is entirely occupied by an albuminous material of a jelly-like consistence, the "corps reticulé" of Velpeau. This substance is separated from the chorion by a thin membrane, the *endochorion;* so that it appears to be contained within a special sac.

The amnion consists of a closed sac, and it is prolonged over the

structures of the cord, in the form of a tubular sheath, which becomes continuous with the integument of the fœtus at the navel. The amnion is tolerably transparent, and not very thick; but often so firm, that it cannot be ruptured very readily. No vessels, nerves, or lymphatics have yet been demonstrated in the healthy membrane; but in some cases of disease it has been found to be highly vascular. M. Coste speaks of the amnion as the "epidermis of the blastoderma."

The sac of the amnion contains a considerable quantity of an albuminous fluid, the *liquor amnii*, which, according to Vogt, consists of common salt, lactate of soda, albumen, and sulphate and phosphate of lime. Dr. G. O. Rees has found urea in the liquor amnii, and the presence of this substance has been confirmed by other observers. The liquor amnii, at three-and-a-half months, had a specific gravity of 1·0182, and contained 10·77 of albumen in 1000 parts; and at six months its specific gravity was 1·0092, and it contained only 6·67 parts of albumen per 1000.

Liquor Amnii.—The liquor amnii enters the mouth of the fœtus, and no doubt passes into the *trachea* as well as the *stomach*; but the amount of nutrition which the fœtus receives from this source, must indeed be small. At the same time, it is interesting to observe, that the composition of the liquor amnii varies at different periods of pregnancy, as has been shown by Vogt; and during the earlier periods of gestation, the quantity of chloride of sodium is much greater than during the latter part of the time. The proportion of this substance appears to be greater at that period of the development of the embryo, when cell-multiplication and growth is most active.

Dr. Beale has made, for Dr. A. Farre, an examination of liquor amnii at the eighth month, taken from the body of a woman who died at this period of gestation. The fluid was of a very pale straw colour, slightly turbid, and contained flocculi suspended in it. It was quite limpid, and readily dropped from a tube. It was very feebly acid, and remained so for several days after it had been removed. The deposit was subjected to microscopical examination, and found to contain many epithelial cells and oil-globules from the *vernix caseosa,* the soft oily coating with which the skin of the fœtus becomes covered in the later months of pregnancy. Besides these, there were several clear, transparent, elongated cylindrical bodies, evidently *casts of the uriniferous tubes* of the kidney of the fœtus. This observation proves, very satisfactorily, that the urinary secretion becomes mixed with the liquor amnii in the human subject.

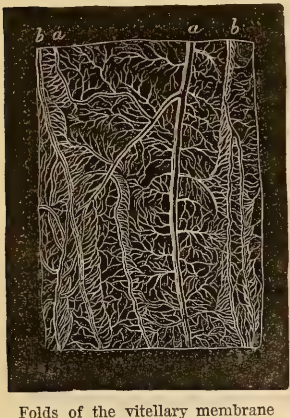
The specific gravity of this specimen was 1009·2, and it contained in 1000 parts—

		In 100 parts solid matter.
Water	982·00	
Solid matter	18·00	
Organic matter soluble in water . . .	6·11	33·94
Fixed alkaline salts	8·09	44·94
Albumen, earthy salts, and fatty matter .	3·80	21·11

Dr. Prout found sugar of milk in the liquor amnii of a cow, at an early period of pregnancy.

Umbilical Vesicle.—We have alluded to the mode of formation of the umbilical vesicle in page 584. Our friend, Mr. Grainger, has made some very important observations on its minute structure and functions in the chick. At a very early period, the lining membrane of the umbilical vesicle presents the appearance of a highly organised mucous membrane, the surface of which is perfectly smooth. After a time, a number of folds, which were termed "valves" by Haller, make their appearance. By the ninth day, these are considerably developed, and project into the yolk. The folds become more complicated and numerous; and by the nineteenth day, are as much as $\frac{5}{12}$ of an inch in depth in the deepest part. Upon the folds, and in the intervals between them, grayish-white corpuscles are very numerous. Mr. Dalrymple has shown that these cells may be washed away from the vessels beneath, of which he has made very beautiful injections. The yellow appearance of the vessels, whence they have been called *vasa lutea* by Haller, is due to their being entirely covered with these yellowish corpuscles. The surfaces of the folds of the membrane are highly vascular, and the majority of the capillaries spread out upon them are probably venous. Thus the surface of the umbilical vesicle is enormously increased in extent, in a manner precisely similar to that in which the mucous membrane of the intestines is extended by the arrangement of the valvulæ conniventes. Such is the character of the vascular surface by which all the nutritive constituents of the yolk are absorbed, which are afterwards carried to the sys-

Fig. 291.



Folds of the vitellary membrane and vasa lutea (after Mr. Dalrymple), showing arrangement of the vessels. From the chick.

tem of the chick for its nutrition, throughout the whole period of development within the shell. That portion of the yolk nearest to the vessels becomes quite fluid, and is therefore in a state most favorable for absorption; it also becomes mixed with the albumen, by which it was originally surrounded, and which enters by endosmosis through the yolk membrane; and it undergoes certain chemical changes, as the experiments of Dr. Prout have shown.

We have already shown (page 584), that the yolk is in direct continuity with the cavity of the intestine, through the intervention of the vitelline duct; and it is therefore possible for the nutrient material to reach the system of the chick by this shorter and more simple course at a very early period of development. Although there can be no doubt of the existence of this tubular communication at one time, it is nevertheless quite certain that throughout the greater part of the period of incubation, the duct is impervious, and the nutrient material of the yoke is absorbed by the vessels ramifying upon the surface of the umbilical vesicle, and is carried by the omphalo-mesenteric vessels to the vascular system of the embryo in the manner above described.

The yolk sac of the *mammalian ovum* has a structure very similar to that of the bird. The communication with the intestine is at first very wide, but soon becomes reduced to a narrow tube, the *omphalo-mesenteric* or *vitelline duct*. The umbilical vesicle generally disappears at a very early period; and in the embryo calf, not more than six lines in length, according to Bischoff, it is only connected with the embryo by a thread-like pedicle, and is of very small size. In the frog it disappears very early; while in carnivorous animals, and also in the rodents, it remains throughout a considerable period of intra-uterine life, and is very highly vascular.

The vessels of the umbilical vesicle are well shown in an embryo of Dr. Sharpey's. The fœtus was $1\frac{1}{20}$ of an inch in length. The vesicle was $\frac{4}{10}$ of an inch in diameter, and the pedicle $\frac{7}{10}$ of an inch long. A beautiful engraving of this embryo will be found in Müller's Physiology, translated by Dr. Baly.

In the human embryo of from two to three lines in length, Müller found the duct of the umbilical vesicle very short and wide, and was able to trace its walls in direct continuity with those of the intestine. Dr. Allen Thomson also testifies to the same fact, and Weber has delineated its blood-vessels. It is very distinct in the human embryo about the twentieth day. It lies between the chorion and amnion, and is filled with a yellowish-white yolk. By the third month, it is about four or five lines in diameter; and

from this time it becomes smaller, and gradually disappears. Mayer has, however, detected both the vesicle and its thread-like pedicle at the full period of gestation.

Development of the Allantois.—At a very early period of development of the mammalian embryo, a collection of cells makes its appearance upon the anterior surface of its caudal extremity. This gradually increases in size, becomes flask-shaped, and a cavity in the interior of the mass becomes visible. The vesicle thus formed rapidly enlarges. It contains fluid; and upon its surface, vessels, which ultimately become the *umbilical vessels,* are seen ramifying. As it grows, these vessels are carried with it towards the inner surface of the chorion. The vessels of the umbilical vesicle waste with this structure; while those conducted to the placenta by the allantois, ultimately become the *two umbilical arteries* and the umbilical vein. In the human embryo, the chief office of the allantois seems to be that of conducting the vessels towards that portion of the chorion which is to become the future *placenta;* and as soon as the connection between the fœtus and the placenta is established, which in the human embryo takes place between the third and fourth weeks, the allantois is no longer distinguishable. Besides this office, however, the allantois receives the secretion from the temporary kidneys, or corpora Wolffiana, previous to the formation of the permanent structures.

In many of the lower animals, however, the allantois is developed to a much greater extent than it is in man. In birds and in several mammalian orders, it forms a very large sac, which completely surrounds the embryo; and in the ruminants it contains many quarts of fluid, towards the termination of intra-uterine life.

The allantois in the chick is readily distinguished before the close of the third day, and appears to be connected with the terminal portion of the intestine. Reichert has carefully investigated its development; and has shown, that it is not developed from the intestine or from the *membrana intermedia,* but arises from two masses of cells, situated at the posterior extremity of the Wolffian bodies, which afterwards coalesce, forming a pear-shaped mass, in which a cavity soon manifests itself. Passing from the Wolffian bodies to the two small masses above referred to, are two lines or threads, which ultimately become the excretory ducts of the former organs.

At an early period, the allantois communicates with a common cavity, or cloaca, into which the ureters, the excretory ducts of the Wolffian bodies, and those of the organs of generation open. This is called the *sinus urino-genitalis.* The allantois grows very rapidly, and ultimately entirely envelopes the embryo with its amnion and yolk, and becomes applied to the inner surface of the membrane of the egg-shell. It is highly vascular, and is, in fact, the respiratory organ of the chick as long as it remains within the shell.

The arrangement of the capillaries has been investigated by our friend,

the late Mr. Dalrymple, who has made some very successful injections of the allantois of the chick. On the outer surface—that which is in immediate contact with the membrane of the shell—the capillaries are exceedingly abundant, and very minute. Mr. Dalrymple compares their arrangement to that of the vessels in the air-cells of the lung of reptiles—a resemblance of great interest, when we consider that in the bird this membrane performs a most important part in aërating the blood; indeed, it is through the intervention of the allantois, that all the respiratory changes taking place in the chick are carried on. The air passes through the pores in the shell and membrane beneath, and thus is brought into contact with the blood ramifying in the vessels of the allantois.

The allantois, as was shown by Reichert and others, is connected with the efferent ducts of the Wolffian bodies, and receives the secretion from these glands.

In the human subject, soon after its formation, a dilatation is observed in that part of the allantois nearest the fœtus. This is the rudiment of the *urinary bladder*. Just at the junction between the vesicular portion and the straight tube which passes from this point to the chorion, a folding or constriction occurs. This indicates the first formation of the *urachus*, which has been erroneously considered to be situated in that part between the vesicle and the fœtus. This latter portion however soon becomes divided into two tubes, one being connected with each Wolffian body. These tubes are ultimately con-

Fig. 292.

Diagrams to show the arrangement of the allantois, and the formation of the placenta in different classes of animals:—

a. A portion of the wall of the uterus. *b.* Chorion. *c.* Allantois. *d.* Umbilical vesicle. *e.* Amnion.

A. In ruminants. The cotyledons, spread out over the internal surface of the uterus, fit into cup-shaped cavities formed by the altered chorion. The allantois is of a very large size, and entirely surrounds the embryo.

B. In the feræ (cat, etc.), the placenta forms a zone which surrounds the embryo like a ring. There are no cotyledons.

C. In rodentia and in the human subject. The placenta is limited to one particular part of the chorion. The allantois is very small, and only distinguished at a very early stage.

verted into the ureters. The ureters and urinary bladder are gradually drawn into the cavity of the pelvis, through the umbilical opening. This process, according to Langenbeck, is completed between the twelfth and twentieth week. The urachus, between the bladder and umbilicus, remains tubular long after this, and even at birth in some few instances; in which cases urine has been known to escape from the umbilicus.

Allantoic Fluid is clear, of a brownish-yellow colour. Its specific gravity varies from 1005 to 1030. It contains alkaline lactates, extractive matters, and ammoniacal salts, with alkaline and earthy phosphates, and chloride of sodium. Besides these, however, there is a definite crystallizable substance peculiar to this fluid, termed *allantoin*, which is closely related to *uric acid;* indeed, it may be prepared artificially from this substance, while *urea* is produced at the same time. The composition of allantoic fluid seems nearly identical with that of the urine of calves while suckling, at which time it contains no hippuric acid. This latter substance, however, makes its appearance in the urine as soon as the animal takes vegetable food. *Uric acid* has been found in the allantoic fluid of birds, by Jacobson.

Fig. 293.

Diagram of uterus, with a fully formed, but very young, ovum.—1. Plug of mucus occupying cervix uteri. 2. Opening of Fallopian tube. 3. Decidua vera. 4. Cavity of uterus, nearly filled with ovum. 5. Decidua reflexa. 6. Chorion. 7. Decidua serotina. 8. Allantois in situation of placenta. 9. Amnion. 10. Umbilical vesicle. 11. Umbilical cord. 12. Space between chorion and amnion, filled with albuminous matter.

Velpeau held that the allantois completely surrounded the human

embryo, as it does in many animals; but this statement has been completely refuted by the researches of Müller, Bischoff, Langenbeck, and others.

Umbilical Cord.—The umbilical cord is the long, narrow pedicle, contained in a tube of the amnion, which connects the fœtus with the placenta. In the advanced embryo, it consists principally of the large vessels, through the intervention of which all the nutrient material absorbed from the blood of the mother is conducted to the system of the fœtus.

At an earlier period of development, the cord is really composed of—

1. The remains of the omphalo-enteric duct, or pedicle of the umbilical vesicle.

2. The vasa omphalo-meseraica, or branches of the mesenteric vessels of the fœtus.

3. The urachus, and all that remains of the allantois.

4. The umbilical vessels; consisting of one umbilical vein, which brings the blood back *from* the placenta, and two umbilical arteries, by which the blood is carried *to* the placenta.

In animals generally, however, there are two veins, as well as two arteries, which are the chief branches of the hypogastric arteries of the fœtus. The circulation of the fœtus has been fully described in page 348.

Birth.—In the human subject, the period of pregnancy lasts about nine solar, or ten lunar, months, or 280 days. It varies, however, within certain limits.

The phenomena of parturition are specially treated of in works on Midwifery; so that a very brief reference to this part of the subject will only be required.

Of the immediate cause of the contraction of the uterus, little is known. Valentin attributes it to the excitement of the organs which always exists at the menstrual periods; and he considers that parturition takes place at the tenth menstrual period. Dr. Tyler Smith has advocated a similar view, and believes that the contractions of the uterus are due to the increased action of the ovaries operating upon the cord through the ovarian nerves, which act as *excitors;* while the uterus is thrown into contraction through the medium of the uterine nerves, which are therefore to be regarded as the *motor* nerves concerned in this *reflex* action. The action of the uterus is no doubt in part due to the stimulus produced by the increasing bulk of its contents.

The fœtus lies in utero with its head downwards during the later

months of pregnancy. The contraction of the thick muscular walls of the uterus tends to force the head upon the os uteri, in consequence of which the circular fibres of the latter gradually relax, and the opening dilates. The membranes are pressed towards the vagina, and protrude through the os, until at length they burst, and the liquor amnii escapes.

At each successive pain, the child's head is forced lower and lower into the vagina. The pains increase in force and frequency, and the uterine contractions are assisted by the voluntary contractions of the abdominal muscles; until at last, in a violent paroxysm of pain, the head is born, and the remainder of the child very quickly follows.

A little hæmorrhage usually occurs immediately after the birth of the child, in consequence of the partial detachment of the placenta. This is followed, however, by contractions; and the placenta itself is forced into the vagina shortly after the birth of the child. With the placenta are also expelled portions of the membrana decidua, the remains of the chorion, and the amnion.

After labour, a considerable quantity of fœtid discharge takes place from the uterus. At first, this is composed principally of blood; but afterwards it becomes paler, and consists chiefly of mucus, with pus corpuscles, and a certain quantity of fluid exudation. The uterus gradually returns to its former volume.

For information upon the questions discussed in the present chapter, the student is referred to the works previously enumerated.

CHAPTER XLIV.

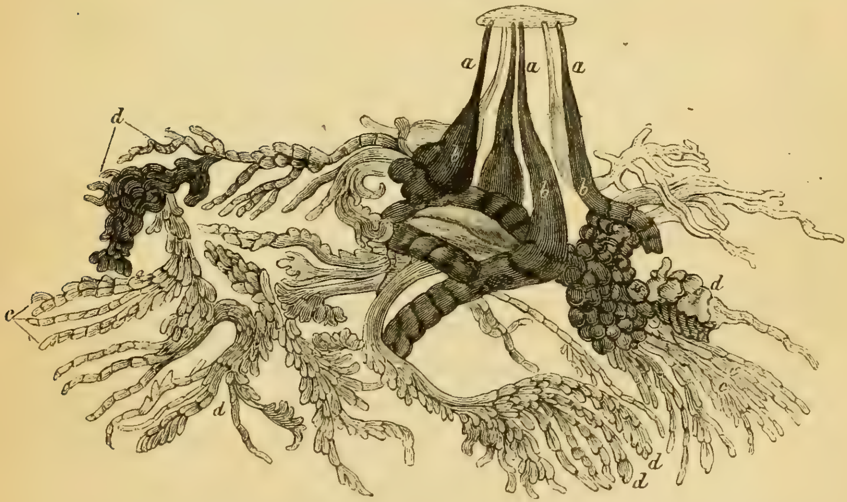
OF LACTATION.—THE LACTEAL GLANDS.—NIPPLE.—MINUTE STRUCTURE OF THE GLAND.—BLOOD-VESSELS.—ABSORBENTS.—MILK.

The *Lacteal Glands* are two large, symmetrical organs, which are only fully developed in the female. In the male, however, they exist in a very rudimentary state. During the later half of pregnancy, the lacteal glands increase very much in size; and about the period of parturition, they begin to secrete milk. They are racemose glands, and are ultimately composed of numerous roundish follicles, arranged round the terminal extremities of the ducts.

The structure of the lacteal glands formed the subject of a very important investigation by Sir Astley Cooper.

The lacteal tubes are about twenty in number, and terminate at the extremity of the nipple, by as many orifices. The ducts are

Fig. 294.



Preparation with six milk-tubes injected from the nipple, by Sir Astley Cooper.—*a.* The straight or mamillary tubes, proceeding from the apex of the nipple. *b.* Reservoirs or dilatations of the ducts. *c.* Branches of the mammary ducts. *d.* Glandules.

dilated as they approach the nipple, and the dilatations are called *reservoirs.* In the human subject, these are very small; but in the cow, they are large enough to hold a quart.

The *nipple* is surrounded by a dark-coloured circle, termed the *areola*, smooth in the child, but slightly tuberculated at the period of puberty. In the child it is about half an inch in diameter; but in the adult, about an inch; while during lactation, it increases to two inches. After impregnation, it changes from its reddish colour to a dark brown.

A secretion is poured out from the mucous follicles, which lubricates the skin about the nipple.

The terminal follicles of the gland were injected by Mascagni; but for almost all that we know of the minute anatomy of the breast, we are indebted to the beautiful researches of Sir Astley Cooper, published in 1840.

The surface of the breasts, in the unimpregnated state, is smooth and compact; but as pregnancy advances, they become uneven, in consequence of the distension of the follicles with secretion.

The nipple, before puberty, forms an almost smooth conical eminence; but in lactation it becomes flattened, so that its extremity becomes the broader part, and thus it is more readily held by the child's mouth. Its characters have been minutely described by Sir Astley Cooper:—"At sixteen years it is slightly wrinkled; at seventeen, it has small papillæ upon its surface; from twenty to forty years, the papillæ are large; from forty to fifty, the nipple becomes wrinkled; from fifty to sixty, the nipple is elongated; and in old age, it usually has a warty appearance."

The cutis of the nipple contains a great number of papillæ. It is sensitive and highly vascular. "The direction of these papillæ is from the base towards the apex of the nipple; so that they are pushed back as the mammilla enters the mouth of the child, and thus greater excitement is produced." Connected with the cutis of the nipple are numerous non-striated muscular fibres, to the presence of which the *erection* of the nipple is due.

In their minute structure, the lacteal glands are closely allied to the pancreas and salivary fluids.

The gland structure is arranged so as to form lobules, which are connected together with a considerable quantity of firm areolar tissue (vol. i. p. 78).

The terminal follicles are about the $\frac{1}{200}$th of an inch in diameter. They are lined with a layer of delicate epithelial cells, which become much altered at the time of lactation. At this time

the cells become larger and much more numerous. They contain a great number of small oil-globules, which constitute, when set free, the oil-globules of the milk. In *colostrum* there are numerous cells of this kind, filled with oil-globules. These have been termed *colostrum* corpuscles, and were first described by Donné. The ducts are lined with columnar epithelium.

The walls of ducts of moderate size are composed of fibrous tissue, in which a great number of elongated, wavy, and nearly parallel fibres of yellow elastic tissue are seen.

Fig. 295.

One of the smallest lobules of a lacteal gland, with ducts, from a puerperal woman; magnified 70 diameters. After Langer.

Fig. 296.

Terminal follicles of the lacteal gland, with ducts, from a woman who was not pregnant. The fibres of yellow elastic tissue are numerous upon the wall of the duct. The terminal follicles are separated from each other by a considerable quantity of areolar tissue. Magnified about 150 diameters.

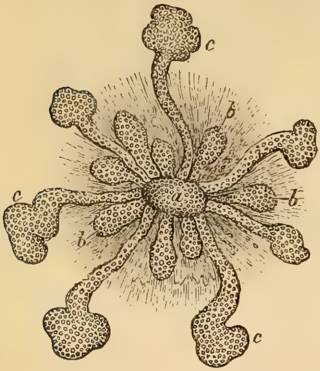
Henle describes muscular fibres in these ducts; but Kölliker and most other anatomists have failed to detect them. We have searched for them carefully, but with no better success.

The *blood-vessels* are very numerous, and their finer branches ramify around the terminal follicles of the gland.

The *absorbents* have been injected by Sir Astley Cooper, who describes a superficial set beneath the skin, and a deeper set of trunks which penetrate into the substance of the gland, and form a plexus of great beauty in the interior."

In the male, the lacteal glands exist only in a very rudimentary condition; but their structure is precisely similar to those of the female, as Sir Astley Cooper demonstrated. In a few very rare instances, they have been unusually developed; and instances are even on record, where milk has been secreted by the lacteal gland of the male; indeed it has been related, by Humboldt, that the infant has been nourished by the male parent after the death of the female.

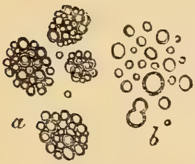
Fig. 297.



Lacteal gland of a newly-born child. The rudimentary follicles are well shown. After Langer.

The lacteal glands are developed like other glands connected with the skin. In the fourth or fifth month, according to the observations of Langer and Kölliker, a papillary projection of the mucous layer of the epidermis occurs. This increases in size; and, by the sixth or seventh month, throws off a number of offsets, from which the lobes of the gland are gradually formed.

Fig. 298.



a. Colostrum corpuscles. *b.* Milk globules. In the lower part of the figure, two are seen running together, in consequence of the investing membrane having been dissolved. Magnified about 215 diameters.

Milk is white and opaque, from the presence of numerous oil-globules. Besides these, which are held in suspension, and are insoluble, milk contains numerous nutritious substances which exist dissolved in the fluid. After it has been allowed to stand for some time, the oil-globules rise to the surface, by reason of their lightness, forming the cream.

Milk usually does not obtain its normal characters until three or four days after delivery. The first proportion, which is secreted before parturition, is thinner, and contains but a

quantity of saccharine and oily materials. In it albumen is often detected. This is called the *colostrum.* The specific gravity varies from 1020 to 1045.

The oil existing in milk, occurs in a state of minute division, in the form of oil-globules, which are equally diffused throughout the fluid. These oil-globules are each invested with a delicate membranous envelope, composed of caseine, which prevents their running together. If milk and ether be shaken and well mixed, the oily constituents are not dissolved, in consequence of the envelope of caseine with which they are invested; but if, previous to the addition of the ether, a little acetic acid or alkali, or alkaline salt, which has the power of dissolving the covering, be added, the globules are immediately dissolved, and the milk becomes perfectly clear. By *churning,* the envelopes are ruptured, and the oil-globules are made to run together, forming *butter.*

If the slightly turbid solution from which the cream has been removed be allowed to stand for some time, or if an acid be added to it, a flocculent precipitate occurs. This is caseine, which is coagulated by all acids. It is, however, not coagulated by heat; but during evaporation, a scum forms upon the surface of solutions containing caseine.

The following analyses show the chemical composition of human milk. Specific gravity, 1030—1034.

	Colostrum.	4 days after parturition.	9 days.	12 days.	Average.
Water	828·0	879·848	885·818	905·809	891·0
Solid matter	172·0	120·152	114·182	94·191	109·0
Albumen	40·0 caseine	35·333	36·912	29·111	33·7
Butter	50·0	42·968	35·316	33·454	37·1
Sugar of milk	70·0	41·135	42·979	31·537	38·5
Salts	3·1	2·095	1·691	1·939	1·9

The first two analyses are by Franz Simon, and the last three by Clemm.

Cow's milk contains more caseine and less sugar than human milk. Ass's milk contains less butter and less caseine, but more sugar; while in goat's milk the caseine preponderates over the other constituents. L'Herctier has shown that temperament exerts an influence upon the character of the milk. The average quantity of solid matter in 1000 parts of milk from fair women, was 120 grains; and of brunettes, as much as 134 grains.

The characters of the milk, also, it need hardly be said, are

much influenced by the health and diet of the mother, and by the age of the infant. At first, the caseine is small in quantity, and gradually increases up to its normal standard; while, on the other hand, the proportion of sugar is very large at first, and subsequently diminishes in quantity. The proportion of butter varies considerably. Phosphate of lime is very soluble in solutions of caseine, and in this way, no doubt, is introduced into the system of the young animal.

In disease, the milk may contain blood, pus, or mucus, and occasionally lactic acid and albumen have been detected in it; urea and bile-pigment have also been found in milk.

Upon the subject of lactation, the student may refer to the following:—On the Anatomy of the Breast, by Sir Astley Cooper, 1839. C. Langer, Ueber den Bau und die Entwicklung der Milchdrüsen, mit 3 Taf., Denkschr. d. Wiener Akad. Bd. iii. Wien. 1851. Article "Mammary Gland," by Mr. Solly, in the Cyclopædia of Anatomy and Physiology. And Simon's Animal Chemistry, translated by the Sydenham Society.

INDEX.

THE END.

The Philosophy of Living.
By Herbert Mayo, M.D. Cheaper Edition. 5s.

Management of the Organs of Digestion.
By the same author. 6s. 6d.

Lunacy and Lunatic Life. 3s. 6d.

German Mineral Waters: and their Employment
for the Cure of certain Chronic Diseases. By S. Sutro, M.D.; Physician to the German Hospital. 7s. 6d.

Spasm, Languor, and Palsy.
By J. A. Wilson, M.D.; Fellow of the College of Physicians; Physician to St. George's Hospital. 7s.

Elements of Chemistry.
By W. A. Miller, M.D., F.R.S.; Professor of Chemistry, King's College.
Part I.—Chemical Physics. 10s. 6d.
Part II.—Inorganic Chemistry. 16s.
Part III.—Organic Chemistry.

Manual of Chemistry.
By W. T. Brande, F.R.S. Sixth Edition, much enlarged. Two large Volumes. £2 5s.

Dictionary of Materia Medica and Pharmacy.
By the same author. 15s.

Principles of Mechanism.
By R. Willis, M.A., F.R.S.; Jacksonian Professor in the University of Cambridge. Second Edition, *in the Press.*

Mechanics applied to the Arts.
By H. Moseley, M.A., F.R.S.; one of Her Majesty's Inspectors of Schools. 6s. 6d.

Lectures on Astronomy.
By the same author. Cheaper Edition, revised. 3s. 6d.

Elements of Meteorology.
By the late Professor Daniel, of King's College. With Plates. Two Volumes, Octavo. 32s.

On Thunderstorms, and on the Means of Protecting
Buildings and Shipping against the Effects of Lightning. By Sir W. Snow Harris, F.R.S. 10s. 6d.

Minerals and their Uses.
By J. R. Jackson, F.R.S. With Frontispiece. 7s. 6d.

Lectures on Dental Physiology and Surgery.
By J. Tomes, F.R.S. Octavo. With 100 Illustrations. 12s.

Use and Management of Artificial Teeth.
By the same author. 3s. 6d.

Practical Geology and Mineralogy.
By Joshua Trimmer, F.G.S. Octavo. With 200 Illustrations. 12s.

Elements of Logic.
By R. Whately, D.D., Archbishop of Dublin. 4s. 6d. Octavo, 10s. 6d.

Elements of Rhetoric.
By the same author. 4s. 6d. Octavo, 10s. 6d.

History of the Inductive Sciences.
By W. Whewell, D.D., F.R.S.; Master of Trinity College, Cambridge. Third and Cheaper Edition. Three Volumes, Crown Octavo.

Philosophy of the Inductive Sciences.
By the same author. Second Edition. Two Volumes, Octavo. 30s.

Atlas of Physical and Historical Geography.
Engraved by J. W. Lowry. 5s.

Manual of Geographical Science.
Part the First. 10s. 6d. Containing:—
Mathematical Geography. By Rev. M. O'Brien.
Physical Geography. By T. D. Ansted, M.A., F.R.S.
Chartography. By J. R. Jackson, F.R.S.
Theory of Description and Geographical Terminology. By Rev. C. G. Nicolay.

History of the Royal Society, compiled from Original Authentic Documents. By C. R. Weld, Assistant Secretary of the Royal Society. Two Volumes. 30s.

The Comets.
By J. Russell Hind. 5s. 6d.

An Astronomical Vocabulary.
By the same author. 1s. 6d.

Cycle of Celestial Objects.
By Admiral W. H. Smyth, Foreign Secretary of the Royal Society. Two Volumes. With Illustrations. £2 2s.

4.A.105